

SYSTEMATICS, PHYLOGENY, AND BIOGEOGRAPHY OF *CHAETOLEPIS* (MELASTOMATACEAE)

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ABSTRACT

Cladistic analyses based on morphology were conducted to test for monophyly, estimate the phylogenetic relationships among the taxa of *Chaetolepis*, and generate the first comprehensive taxonomic revision of the genus. Prior to this study the genus had included species from Andean South America, the Guayana Highlands, Costa Rica, Cuba, and tropical West Africa. As traditionally delimited, *Chaetolepis* is not monophyletic because the Cuban species, *C. cubensis*, is more closely related to outgroup species in the genus *Tibouchina*. Based on discordant morphological characters such as foliar trichome details and seed morphology, *C. cubensis* is here treated as a *Tibouchina*, the genus to which it had been transferred by M. Gómez in 1894. *Chaetolepis* is treated as a monophyletic genus of 11 species distinguished by 4-merous flowers, isomorphic stamens that lack prominent pedoconnectives and appendages, apically setose 4-locular ovary, capsular fruits, and cochleate seeds. *Chaetolepis alpina* var. *latifolia* is relegated to synonymy of *C. alpina* because it lacks consistent distinguishing characters, and *C. thymifolia* is synonymized under *C. anisandra*. The West African monotypic genus, *Nerophila gentianoides*, is tentatively shown to be congeneric with the Central and South American species of *Chaetolepis* based on morphology. If molecular data confirms this disposition of *N. gentianoides* by Jacques-Félix, it will become the only genus of Melastomataceae with a trans-Atlantic distribution. A biogeographical analysis based on the phylogenetic results suggests that *Chaetolepis* originated in the Colombian Andes and possibly the Sierra Nevada de Santa Marta, with independent dispersal events to Costa Rica, Venezuela, and tropical West Africa.

RESUMEN

Se llevaron a cabo Análisis cladísticos basados en morfología para probar la monofilia, estimar las relaciones filogenéticas entre los taxones de *Chaetolepis*, y generar la primera revisión taxonómica completa del género. Antes de este estudio el género había incluido las especies de los Andes de América del Sur, las tierras altas de Guayana, Costa Rica, Cuba, y tropicales de África occidental. Como se ha delimitado tradicionalmente, *Chaetolepis* no es monofilético ya que la especie cubana, *C. cubensis*, está más estrechamente relacionada con la especie del grupo externo del género *Tibouchina*. Se trata aquí en base a caracteres morfológicos discordantes como los detalles de tricomas foliares y morfología de la semillas como una *Tibouchina*, *C. cubensis*, el género al que había sido trasladado por M. Gómez en 1894. *Chaetolepis* se trata como un género monofilético de 11 especies que se distinguen por sus flores con 4 pétalos, estambres isomorfos que carecen de pedoconnectivos prominentes y apéndices, los ovarios apicalmente setosos 4-loculares, frutos capsulares y semillas cocleadas. *Chaetolepis alpina* var. *latifolia* se sinonimiza a *C. alpina* porque carece de caracteres distintivos constantes, y *C. thymifolia* se sinonimia a *C. anisandra*. El género monotípico de África Occidental, *Nerophila gentianoides*, está tentativamente demostrado ser congenérico con las especies centro y sudamericanas de *Chaetolepis* basado en la morfología. Si los datos moleculares confirman esta disposición de *N. gentianoides* por Jacques-Félix, será el único género de Melastomataceae con una distribución transatlántica. Un análisis biogeográfico basado en los resultados filogenéticos sugiere que *Chaetolepis* se originó en los Andes colombianos y, posiblemente, la Sierra Nevada de Santa Marta con eventos de dispersión independientes a Costa Rica, Venezuela, y África occidental tropical.

INTRODUCTION

Chaetolepis Miq. (Melastomataceae) is a small mostly neotropical genus of montane shrubs and subshrubs (rarely annuals). As interpreted here, it consists of 11 species that are readily characterized by 4-merous, diplostemonous flowers, isomorphic mostly inappendiculate stamens that lack well-developed pedoconnectives, 4-locular, apically setose ovaries, and cochleate seeds with a testa that consists mostly of compressed/flattened interdigitating cells. The genus, as it has been circumscribed in the past, has included species of Andean South America, the Guayana Highlands, southern Central America, and Cuba. Recently, the monotypic genus *Nerophila* Naudin, from west tropical Africa was transferred to *Chaetolepis* (Jacques-Félix 1995). No previous study has attempted to evaluate *Chaetolepis* or *Nerophila*. Because the monophyly of the geographically disparate assemblage of taxa referred to *Chaetolepis* had never been evaluated, it seemed ripe for testing.

The primary goals of this study were to determine if *Chaetolepis* is monophyletic, assess the phylogenetic relationships of the constituent species based on morphology, and evaluate character evolution by using cladistic techniques. A taxonomic revision is provided that includes detailed descriptions of all recognized taxa, scanning electron microscope images of seeds for selected species, a summary of known chromosome numbers, information on habitat and geographic distributions, flowering phenology, distribution maps, illustrations of all recognized species, citations of specimens examined, and a list of excluded taxa. This was supplemented by limited field study of four species in Costa Rica, Colombia, and Venezuela.

Tribal and Generic Affinities.—*Chaetolepis* belongs to the tribe Melastomeae, the core members of which are characterized by cochleate seeds with a testa that is tuberculate or papillate, a crown of trichomes or appendages on the ovary apex, and the presence of staminal pedoconnectives (Renner and Meyer 2001; Freire-Fierro 2002; Michelangeli et al. 2013). Based on overall morphological similarities, Wurdack (1973) hypothesized that *Chaetolepis* is most closely related to *Tibouchina* Aubl. No cladistic analyses or molecular data, however, had been used to assess the possible sister relationships of *Chaetolepis*. Other neotropical relatives of *Chaetolepis* include *Aciotis* D. Don, *Arthrostemma* Pav. ex D. Don, *Heterocentron* Hook & Arn., *Microlicia* D. Don, *Microlepis* (DC.) Miq., *Monochaetum* (DC.) Naudin, *Nepsera* Naudin, *Pterolepis* (DC.) Miq., and *Rhexia* L. based on a study using *ndhF* and *rpl16* cpDNA sequences of 24 members of Melastomeae and outgroups (Renner and Meyer 2001). Based on an expanded molecular sampling using DNA sequence data, *Bucquetia* DC., *Castratella* Naudin, and *Monochaetum* are now considered the closest sister taxa of *Chaetolepis* (Penneys et al. 2010; Michelangeli et al. 2013). Like *Chaetolepis*, the majority of species in these genera are also restricted to higher elevation montane environments in the Andes of northwestern South America and all have tetramerous flowers, an apically setulose ovary that is four locular and free from the hypanthium, and capsular fruits.

Comparative Morphology (Characters of Taxonomic Value).—The species of *Chaetolepis* are easily distinguished from each other by characters involving the indument, anther connective, seed surface, petal coloration, and petal margin. The indument found on leaves, internodes, nodes, and floral organs includes eglandular trichomes, glandular trichomes, barbellate/dendritic trichomes, and scales. The distribution of the indument on the vegetative and floral structures varies greatly. It ranges from absent to densely covering the surfaces of vegetative and floral organs. The anther connective prolongation ranges from absent to minutely prolonged (<1mm). It can also be unappendaged, minutely bilobed (<1mm) on the ventral side of the connective, or with a minute dorsal appendage. The seed surface is prevalingly smooth with compressed/flattened interdigitating cells or with elongate somewhat convex interdigitating cells. The petals vary in color from yellow to pink or magenta and their margins are either glabrous or ciliate.

Taxonomic History.—*Chaetolepis* has been treated as a distinct genus since Miquel (1840) characterized the group. Since then several species have been variously treated in monographic (Cogniaux 1891) and regional floristic studies (Standley 1938; Uribe-U. 1972; Wurdack 1973; Almeda 2001). Over the past 80 years some of the species have been described in geographical accounts of the genus and some authors have commented on the placement of *Chaetolepis* species that had been described in other genera (Standley 1938; Wurdack 1973; León and Alain 1974; Martins 1989). Prior to the current study, *Chaetolepis* was believed to comprise 13 species and three varieties. Because all previous studies were largely regional in nature, no attempt was made to identify synapomorphies and only cursory attention was given to the importance and/or variation of certain vegetative and reproductive characters. In Cogniaux's (1891) monograph of Melastomataceae, for example, some of the characters used to characterize *Chaetolepis* included 4-merous flowers; ovate to obovate petals varying in color from rose to purple; 4-locular ovaries with a setose apex; minimally prolonged unappendaged connectives; and ovoid cochleate seeds with smooth surfaces. Almeda's (2001) more recent generic description of a smaller sampling of species is similar but he noted that the petals range from yellow, magenta, to purple and the seed surface appears "smooth or finely and diminutively muriculate." No prior work mentioned any sculptural details of the seed testa because no SEM studies had been attempted. This lack of consistency and detail relating to the seed and other structures may have led to the placement of unrelated species in *Chaetolepis*, perhaps biased by the four-merous flowers and greatly reduced pedoconnective. Furthermore, some

doubt about the monophyly of the genus has persisted because no cladistic analysis of the group has ever been undertaken to evaluate character states and their evolution.

MATERIALS AND METHODS

I. Cladistic and Biogeographic Analyses

Ingroup.—All sixteen taxa thought to comprise *Chaetolepis* form the ingroup for this study. *Chaetolepis alpina* var. *alpina*, *C. alpina* var. *latifolia*, *C. anisandra*, *C. cubensis*, *C. cufodontisii*, *C. gentianoides*, *C. lindeniana*, *C. loricaella*, *C. microphylla*, *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. phelpisiae* var. *phelpisiae*, *C. phelpisiae* var. *chimantensis*, *C. santamartensis*, *C. sessilis*, and *C. thymifolia*.

Outgroup.—To assess the monophyly of *Chaetolepis*, seven species among the genera *Tibouchina*, *Microlicia*, and *Monochaetum* were used as the outgroup. The exemplars used were *T. gleasoniana* Wurdack, *T. narinoensis* Wurdack, *T. wurdackii* Almeda and Todzia, *Microlicia canastrensis* Naudin, *M. obtusifolia* Cogn. ex R. Romero, *Monochaetum amabile* Almeda, and *M. compactum* Almeda. *Tibouchina* was chosen as part of the outgroup because Wurdack (1973) hypothesized that it likely shares a most recent common ancestor with *Chaetolepis* based on many shared characteristics, such as perigynous flowers, campanulate or urceolate hypanthia, superior ovaries that are apically pubescent, capsular fruits, and cochleate seeds. In addition, *T. gleasoniana*, *T. narinoensis*, and *T. wurdackii* were chosen as part of the outgroup because the tuberculate seed testa and foliar scales (see Todzia and Almeda 1991) are identical to those found in *C. cubensis*. The species of *Microlicia* and *Monochaetum* were chosen as other members of the outgroup because of their close phylogenetic proximity to *Tibouchina* based on molecular studies by Renner and Meyer (2001).

Material Examined.—Over 400 herbarium specimens, including types, were used in the phylogenetic analysis and taxonomic revision. Specimens from the following herbaria with significant holdings of Central and South American Melastomataceae were borrowed or studied on site: BM, BR, CAS, COL, DS, DUKE, F, FMB, G, GH, HECASA, K, M, MO, NY, P, US, and UTM (acronyms according to Thiers 2012). Internet images of type specimens (JSTOR Plant Science) were examined for those taxa that were not readily available on loan.

Characters.—Forty-one vegetative and floral characters were used in the analysis (Tables 1 and 2). The type of indument covering both vegetative and floral structures was particularly informative in this study.

Data Analysis.—The software program PAUP* 4.0b10 (Swofford 2002) was used to generate phylogenetic estimates. Maximum parsimony with a branch and bound search was selected to evaluate the data matrix that was generated in MacClade 4.03 (Maddison and Maddison 2000). Two analyses were conducted. Analysis 1 was performed to assess the monophyly of *Chaetolepis* and analysis 2 provided insight into ingroup relationships after the exclusion of one of the species of *Chaetolepis* (*C. cubensis*) was prompted by the results of the first analysis. The first analysis used 41 morphological characters and 23 taxa. Sixteen species formed the presumed ingroup and seven species from the genera *Tibouchina*, *Monochaetum*, and *Microlicia* formed the outgroup. Default options were used to run the analysis. In analysis 2, a backbone constraint was applied that grouped all outgroup members plus *C. cubensis* together because of their unique floral and/or seed characters and grouped all ingroup taxa together. This was done by constructing a tree in MacClade (Maddison & Maddison 2000) with the data matrix, opening the file in PAUP (Swofford 2002), derooting the tree, loading the tree as a backbone constraint in the analysis, and finally enforcing the constraint in the search.

To evaluate the strength of the different clades in the various phylogenies generated, a bootstrap analysis employing a heuristic search was utilized in PAUP. Stepwise-addition branch swapping was employed; otherwise, default options were used.

MacClade was used to infer the evolution of characters among the lineages of *Chaetolepis*. The “trace,” “all changes,” and “all possible changes” options were chosen.

To gain insight into the historical biogeography of *Chaetolepis*, two analyses were conducted. The first was performed to provide insight into the origin and dispersal patterns of the different taxa within South America, Central America, and Africa. This analysis used Fitch optimization in MacClade, a data matrix incorporating all *Chaetolepis* taxa, a single area character with four states representing different geographic areas

TABLE 1. Morphological characters and character states used in the phylogenetic analysis of *Chaetolepis*.

1. Hypanthium base (glands): no glands (0); punctate, with depressions (1); sessile glands (2).
2. Hypanthium base (trichomes): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated, slightly to greatly barbellate trichomes (3).
3. Hypanthium base (scales): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2).
4. Hypanthium apex (glands): no glands (0); punctate, with depressions (1); sessile glands (2).
5. Hypanthium apex (trichomes): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated, slightly to greatly barbellate trichomes (3).
6. Hypanthium apex (scales): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2).
7. Leaf margin: glabrous (0); ciliate (1).
8. Leaf margin (pattern): crenulate (0); serrulate (1); entire (2).
9. Adaxial leaf surface (glands): no glands (0); punctate, with depressions (1); sessile glands (2).
10. Adaxial leaf surface (trichomes): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to greatly barbellate trichomes (3); bulla-based trichomes (4).
11. Adaxial leaf surface (scales): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2); appressed, lanceolate, flattened scales, attached entire length of scale, erose margin (3); appressed, lanceolate, flattened scales, basally attached, entire margin (4); flattened scales adnate for $\frac{1}{3}$ to $\frac{2}{3}$ their length, distal region of scales free and triangular (5).
12. Abaxial leaf surface (glands between primary veins): no glands (0); punctate, with depressions (1); sessile glands (2).
13. Abaxial leaf surface (trichomes between primary veins): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to greatly barbellate trichomes (3); variously branched and terete (4).
14. Abaxial leaf surface (scales between primary veins): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally or basally attached without a raised thickening near the point where scale attaches to surface, erose margin (2); appressed, lanceolate, flattened scales, attached entire length of scale, erose margin (3); appressed, lanceolate, flattened scales, basally attached, entire margin (4); flattened scales adnate for $\frac{1}{3}$ – $\frac{2}{3}$ their length, distal region of scales free and triangular (5).
15. Abaxial leaf surface (glands on primary veins): no glands (0); punctate, with depressions (1); sessile glands (2).
16. Abaxial leaf surface (trichomes on primary veins): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to greatly barbellate trichomes (3).
17. Abaxial leaf surface (scales between primary veins): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally or basally attached without a raised thickening near the point where scale attaches to surface, erose margin (2); appressed, lanceolate, flattened scales, attached entire length of scale, erose margin (3); appressed, lanceolate, flattened scales, basally attached, entire margin (4); flattened scales adnate for $\frac{1}{3}$ – $\frac{2}{3}$ their length, distal region of scales free and triangular (5).
18. Branch surface internodes (glands): no glands (0); punctate, with depressions (1); sessile glands (2).
19. Branch surface internodes (trichomes): no trichomes (0); smooth eglandular trichomes, sparsely pubescent (1); smooth glandular trichomes, sparsely pubescent (2); smooth eglandular trichomes, moderately to densely pubescent (3); smooth glandular trichomes, moderately to densely pubescent (4); elongated slightly to greatly barbellate trichomes (5).
20. Abaxial leaf surface (scales between primary veins): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally or basally attached without a raised thickening near the point where scale attaches to surface, erose margin (2); appressed, lanceolate, flattened scales, attached entire length of scale, erose margin (3); appressed, lanceolate, flattened scales, basally attached, entire margin (4); flattened scales adnate for $\frac{1}{3}$ – $\frac{2}{3}$ their length, distal region of scales free and triangular (5).
21. Branch surface nodes (glands): no glands (0); punctate, with depressions (1); sessile glands (2).
22. Branch surface nodes (trichomes): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to copiously barbellate trichomes (3).
23. Abaxial leaf surface (scales between primary veins): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally or basally attached without a raised thickening near the point where scale attaches to surface, erose margin (2); appressed, lanceolate, flattened scales, attached entire length of scale, erose margin (3); appressed, lanceolate, flattened scales, basally attached, entire margin (4); flattened scales adnate for $\frac{1}{3}$ – $\frac{2}{3}$ their length, distal region of scales free and triangular (5).
24. Intercalary lobe sinus (trichomes): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated, slightly to greatly barbellate trichomes (3); forked (4); stalked and variously branched trichomes (5).
25. Intercalary lobe sinus (scales): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2).
26. Calyx vestiture (glands found on structure except midrib): no glands (0); punctate, with depressions (1); sessile glands (2).

27. Calyx vestiture (trichomes, excluding midrib): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to copiously barbellate trichomes (3).
28. Calyx vestiture (scales, excluding midrib): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2).
29. Calyx vestiture (glands found on midrib): no glands (0); punctate, with depressions (1); sessile glands (2).
30. Calyx vestiture (trichomes found on midrib): no trichomes (0); smooth eglandular trichomes (1); smooth glandular trichomes (2); elongated slightly to copiously barbellate trichomes (3).
31. Calyx vestiture (scales found on midrib): no scales (0); appressed, ovate, flattened scales, basally attached with a raised thickening near the point where scale attaches to surface, erose margin (1); appressed, lanceolate flattened scales, proximally attached without a raised thickening near the point where scale attaches to surface, erose margin (2).
32. Androecium: isomorphic (0); dimorphic (1).
33. Connective: not prolonged or minutely prolonged (<1mm) and no appendages (0); minutely prolonged <1mm and with 2 ventral appendages or thickenings <1mm (1); prolonged >1mm and with 2 ventral appendages >1mm (2); prolonged >1mm and with 2 dorsal appendages >1mm (3); not prolonged with dorsal appendage (4).
34. Apical pore orientation: ventral (0); dorsal (1).
35. Ovary apex: glabrous and non-punctate (0); smooth eglandular trichomes (1); barbellate trichomes (2).
36. Seed Shape: cochleate (0); reniform (1).
37. Seed testa: smooth with compact, interdigitating cells (0); smooth with elongate, interdigitating cells (1); tuberculate (2); foveolate (3).
38. Leaf primary veins: mostly 1 (0); mostly 3 (1); mostly 5 (2).
39. Merosity: typically 4 (0); typically 5 (1).
40. Petal margin: glabrous or with a terminal trichome (0); ciliate (1).
41. Petal color: yellow (0); ranging from pink, purple, to magenta (1).

in which they are found (Table 3), and one of the 26 most parsimonious tree topologies generated in PAUP with polytomies resolved arbitrarily. The second analysis was performed to infer how *Chaetolepis* taxa may have migrated within the Andes. This analysis differed from the first analysis only in the number of area states (five) used. In the analysis, all equally most parsimonious reconstructions (MPR's) were examined.

II. Chromosome Cytology

Floral bud material was collected in the field, fixed in modified Carnoy's (Bradley 1948) solution (4 chloroform, 3 ethanol, 1 glacial acetic acid, v/v/v) for 24 hours, transferred to 70% ethanol and stored under refrigeration until studied. The new chromosome count reported here for *Chaetolepis cufodontisii* was made from acetocarmine smears of pollen mother cells using a Zeiss light microscope with phase contrast and a 100x oil immersion objective. Drawings of meiotic figures were made by camera lucida at a magnification of 2100x. The voucher collection for this new count is marked with an asterisk among specimens cited.

III. Taxonomic Revision

A dissecting microscope was used to measure all vegetative and reproductive characters based on dried herbarium material. Reproductive characters were taken from either one mature open flower in the center of an inflorescence or a solitary flower at the apex of a flowering branch for each specimen examined. Leaf characters were scored from mature branches. To ensure that aberrant characteristics were not being recorded, numerous specimens were examined and those with typical traits were used.

A scanning electron microscope (SEM) was used to study the seed morphology of each *Chaetolepis* species. Seeds were affixed to aluminum stubs with double-stick tape and sputter-coated with gold-palladium alloy. Samples were photographed in the scanning electron microscope laboratory at the California Academy of Sciences using a Leo 1450 BP scanning electron microscope at 20kV. Voucher collection data for the SEM images are provided in the relevant figure legends.

RESULTS

I. Cladistic Analyses

Phylogeny.—In the first cladistic analysis, 22 most parsimonious trees, each 136 steps long, were generated. The consistency index was 0.66 and the retention index was 0.79. In the strict consensus tree (Fig. 1), 11

TABLE 2. Morphological character states for species of *Chaetolepis* and the seven outgroup taxa. Polymorphic states are represented as #/ # (ex-0/1).

Species	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>C. alpina</i> var. <i>alpina</i>	2	0	0	2	0	0	1	0	2	0	0	1	0	0	2	1	0	2	0	0
<i>C. alpina</i> var. <i>latifolia</i>	2	0	0	2	0	0	1	0	2	0	0	1	0	0	2	1	0	2	0	0
<i>C. anisandra</i>	0	0	0	0	0/1	0	1	0	0	1	0	2	1	0	2	1	0	0	3/4	0
<i>C. cubensis</i>	0	0	2	0	0	2	1	2	0	0	5	0	0	2	0	0	2	0	0	2
<i>C. cufodontisii</i>	2	0	0	2	0	0	0	1	2	0	0	1	0	0	0	1	0	0	0	0
<i>C. gentianoides</i>	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	1	0	0	1	0
<i>C. lindeniana</i>	0	3	0	0	3	0	1	2	0	4	0	0	3	0	0	3	0	0	5	0
<i>C. loricarella</i>	0	0	1	0	0	1	1	2	0	0	1	0	0	1/2	0	0	1	0	0	1
<i>C. microphylla</i>	0	0	0	0	0	0	1	2	0	3	0	0	3	0	0	3	0	0	5	0
<i>C. perijensis</i> var. <i>perijensis</i>	2	0	0	2	0	0	1	2	2	0	0	1	0	0	1	0	0	2	0	0
<i>C. perijensis</i> var. <i>glandulosa</i>	2	2	0	2	2	0	1	2	2	0	0	1	0	0	1	0	0	2	0	0
<i>C. phelpsiae</i> var. <i>phelpsiae</i>	0	1	0	0	1	0	1	0	0	1	0	1	1/2	0	0	1/2	0	0	1/2	0
<i>C. phelpsiae</i> var. <i>chimantensis</i>	0	0	0	0	1	0	1	0	0	1	0	1	1/2	0	0	1/2	0	0	1/2	0
<i>C. santamartensis</i>	0	3	0	0	0	0	1	2	0	3	0	0	3	0	0	3	0	0	5	0
<i>C. sessilis</i>	2	1	0	2	1	0	0	1	0	0	0	1	0	0	0	0	0	2	0	0
<i>C. thymifolia</i>	0	0	0	0	0/1	0	1	0	0	1	0	2	1	0	0	1	0	0	3/4	0
<i>Tibouchina gleasoniana</i>	0	0	2	0	0	2	1	2	0	4	0	0	4	2	0	0	2	0	0	2
<i>Tibouchina narinoensis</i>	0	0	2	0	0	2	1	2	0	4	0	3	0	4	0	0	4	0	0	2
<i>Tibouchina wurdackii</i>	0	0	2	0	0	2	1	2	0	0	5	0	0	2	0	0	2	0	0	2
<i>Microlicia canastrensis</i>	2	2	0	2	2	0	1	2	2	0	0	0	2	0	2	0	0	2	2	0
<i>Microlicia obtusifolia</i>	1/2	0	0	2	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0
<i>Monochaetum amabile</i>	0	1	0	0	1	0	1	2	0	1	0	0	1	0	0	1	0	0	1	0
<i>Monochaetum compactum</i>	0	1/2	0	0	1/2	0	1	2	0	3	0	0	1	0	0	1	0	0	3	0

clades have bootstrap (BS) values greater than 50%. Clade A includes all *Chaetolepis* taxa and the outgroups *Monochaetum amabile*, *M. compactum*, *Tibouchina gleasoniana*, *T. narinoensis*, and *T. wurdackii* (BS=81). Clade B includes all *Chaetolepis* taxa except *C. perijensis* var. *perijensis* and *C. perijensis* var. *glandulosa* and includes the outgroups from the genera *Monochaetum* and *Tibouchina* (BS=71). Clade C consists of all *Chaetolepis* taxa except *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa* and *C. sessilis* and includes the outgroups from the genera *Monochaetum* and *Tibouchina* (BS<50). Clade D consists of all *Chaetolepis* taxa except *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. sessilis*, *C. alpina* var. *alpina*, and *C. alpina* var. *latifolia* and includes the outgroups from the genera *Monochaetum* and *Tibouchina* (BS<50). Clade E contains all *Chaetolepis* taxa except *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. sessilis*, *C. alpina* var. *alpina*, *C. alpina* var. *latifolia*, and *C. cufodontisii* and includes outgroups from the genera *Monochaetum* and *Tibouchina* (BS=53). Clade F is composed of the taxa *C. cubensis*, *T. gleasoniana*, *T. narinoensis*, *T. wurdackii*, and *C. loricarella* (BS=94). Clade G includes *C. cubensis*, *T. gleasoniana*, *T. narinoensis*, and *T. wurdackii* (BS=80). Clade H includes *C. gentianoides*, *C. phelpsiae* var. *phelpsiae*, *C. phelpsiae* var. *chimantensis*, and the outgroups *Monochaetum amabile* and *M. compactum* (BS<50). Lastly, clade I consists of *C. lindeniana*, *C. santamartensis*, and *C. microphylla* (BS=63).

In the second cladistic analysis, 26 most parsimonious trees 148 steps long were generated. The consistency index was 0.61 and the retention index was 0.74. In the strict consensus tree (Fig. 2), 12 clades have bootstrap values greater than 50%. Clade A includes all *Chaetolepis* taxa and the outgroups *Monochaetum amabile*, *M. compactum*, *Tibouchina gleasoniana*, *T. narinoensis*, and *T. wurdackii* and is the backbone constraint. Clade B consists of all *Chaetolepis* taxa except for *C. cubensis* and *Monochaetum amabile* and *M. compactum* (BS=73). Clade C includes all *Chaetolepis* taxa except for *C. cubensis* (BS=100). Clade D includes *C. alpina* var. *alpina* and *C. alpina* var. *latifolia*, *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. sessilis*, and *C. cufodontisii* (BS=58). Clade E includes *C. anisandra*, *C. thymifolia*, *C. gentianoides*, *C. phelpsiae* var. *phelpsiae*, and *C. phelpsiae* var. *chimantensis* (BS=71). Lastly, clade F, includes *C. lindeniana*, *C. santamartensis*, and *C. microphylla* (BS=70).

In one of 26 most parsimonious trees generated in the second cladistic analysis showing how characters change (Fig. 3), clade A is supported by five ambiguous characters. The characters that support this clade

TABLE 2. (continued) Morphological character states for species of *Chaetolepis* and the seven outgroup taxa. Polymorphic states are represented as #/ # (ex-0/1).

Species	Characters																				
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
<i>C. alpina</i> var. <i>alpina</i>	0	1	0	1	0	2	0	0	2	0	0	0	0	1	1	0	0	1	0	0	0
<i>C. alpina</i> var. <i>latifolia</i>	0	1	0	1	0	2	0	0	2	0	0	0	0	1	1	0	0	1	0	0	0
<i>C. anisandra</i>	0	1	0	1/4	0	0	0	0	0	1/2	0	0	0	1	1	0	0	1/2	0	0	0
<i>C. cubensis</i>	0	0	2	0	2	0	0	2	0	0	2	0	1	0	0	0	2	1	0	1	1
<i>C. cufodontisii</i>	0	1	0	1	0	2	0	0	0	1	0	0	0	1	1	0	0	1	0	0	0
<i>C. gentianoides</i>	0	1	0	5	0	0	1	0	0	0	0	0	0	1	1	0	1	2	0	0	0
<i>C. lindeniana</i>	0	3	0	3	0	0	3	0	0	3	0	0	4	1	2	0	0	1	0	1	1
<i>C. loricarella</i>	0	0	1	0	1	0	0	1	0	0	1	0	0	1	2	0	0	0	0	1	1
<i>C. microphylla</i>	0	1/3	0	1	0	0	0	0	0	3	0	0	0	0	1	0	0	1	0	0	0
<i>C. perijensis</i> var. <i>perijensis</i>	2	0	0	1	0	2	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0
<i>C. perijensis</i> var. <i>glandulosa</i>	2	0	0	1	0	2	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0
<i>C. phelpsiae</i> var. <i>phelpsiae</i>	0	1	0	4	0	2	1/2	0	0	1/2	0	0	0	1	1	0	0	1/2	0	0	0
<i>C. phelpsiae</i> var. <i>chimantensis</i>	0	1	0	4	0	2	1/2	0	0	1/2	0	0	0	1	1	0	0	1/2	0	0	0
<i>C. santamartensis</i>	0	3	0	3	0	0	3	0	0	3	0	0	1	1	1	0	0	2	0	1	1
<i>C. sessilis</i>	0	1	0	4	0	2	0	0	2	0	0	0	0	0	1	0	0	1	0	0	0
<i>C. thymifolia</i>	0	1	0	1/4	0	0	0	0	0	1/2	0	0	0	1	1	0	0	1/2	0	0	0
<i>Tibouchina gleasoniana</i>	0	0	4	0	2	0	0	2	0	0	2	0	2	0	1	0	2	2	1	1	1
<i>Tibouchina narinoensis</i>	0	0	2	0	2	0	0	2	0	0	2	0	2	0	1	0	2	2	1	1	1
<i>Tibouchina wurdackii</i>	0	0	2	0	2	0	0	2	0	0	2	1	2	0	1	0	2	1	1	1	1
<i>Microlicia canastrensis</i>	2	2	0	2	0	2	2	0	2	2	0	1	2	0	0	1	3	1	1	0	1
<i>Microlicia obtusifolia</i>	1	0	0	0	0	2	0	0	2	0	0	1	2	0	0	1	3	1	1	0	1
<i>Monochaetum amabile</i>	0	1	0	1	0	0	1	0	0	1	0	1	3	1	1	0	3	1	0	0	1
<i>Monochaetum compactum</i>	0	3	0	1/2	0	1	1/2	0	0	1/2	0	1	3	1	1	0	3	2	0	0	1

TABLE 3. Taxa with four area character states used in the first Fitch optimization analysis, and five area character states used in the second Fitch optimization analysis. Area character states used in the first analysis are: Eastern Cordillera of the Andes (1), Tepuis of Venezuelan Guayana (2), Costa Rica, Talamanca Cordillera (3), and West Africa, Loma Mountains (4). Area character states used in the second analysis are: Sierra Nevada de Santa Marta (1), Eastern Cordillera of the Andes (2), Tepuis of Venezuelan Guayana (3), Costa Rica, Talamanca Cordillera (4), and West Africa, Loma Mountains (5).

Taxa	Area character states used in first Fitch optimization analysis	Area character states used in second Fitch optimization analysis
<i>C. alpina</i> var. <i>alpina</i>	1	1&2
<i>C. alpina</i> var. <i>latifolia</i>	1	1
<i>C. anisandra</i>	1&2	2&3
<i>C. cufodontisii</i>	3	4
<i>C. gentianoides</i>	4	5
<i>C. lindeniana</i>	1	2
<i>C. loricarella</i>	1	1
<i>C. microphylla</i>	1	2
<i>C. perijensis</i> var. <i>perijensis</i>	1	2
<i>C. perijensis</i> var. <i>glandulosa</i>	1	2
<i>C. phelpsiae</i> var. <i>phelpsiae</i>	2	3
<i>C. phelpsiae</i> var. <i>chimantensis</i>	2	3
<i>C. santamartensis</i>	1	2
<i>C. sessilis</i>	1	2
<i>C. thymifolia</i>	1	2

include an androecium that is dimorphic (character 32); a prolonged connective with ventral or dorsal appendages (character 33); a ventral apical pore orientation (character 34); foveolate or tuberculate seed testa (character 37); and five-merous flowers (character 39). Clade B, which is composed of all *Chaetolepis* taxa except for *C. cubensis*, is supported by the same five ambiguous characters. There are 13 characters that support clade

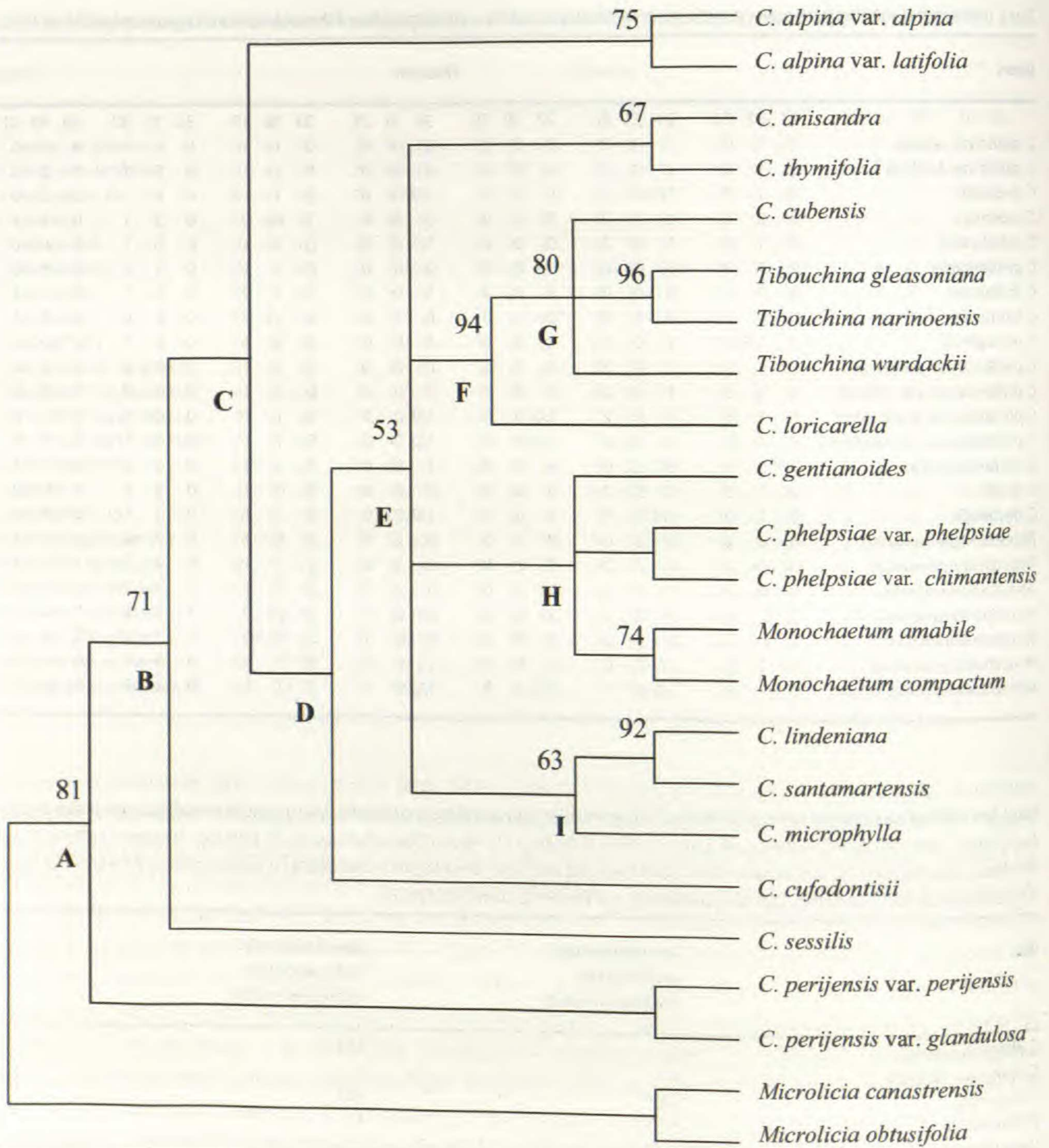


FIG. 1. Strict consensus tree generated from a branch and bound analysis of morphological characters (analysis 1). Bootstrap values greater than 50% are shown above the branches. Letters represent the nodes above them.

C1, of which nine are unique, three are homoplasious and one is ambiguous. The unique characters include appressed, ovate, flattened scales, basally attached with a raised thickening near the point where the scale is attached to the leaf surface and an erose margin on the hypanthium base, hypanthium apex, adaxial leaf surface, abaxial leaf surface primary veins, branch surface internodes, branch surface nodes, intercalycine lobe sinus, calyx vestiture excluding the midrib, and calyx midrib (characters 3, 6, 11, 17, 20, 23, 25, 28, 31 respectively). There are 4 characters that support clade C2, of which three are ambiguous and one is homoplasious (characters 16, 22, 24, and 41). The ambiguous characters are smooth eglandular trichomes, smooth glandular trichomes, or barbellate/dendritic trichomes on the abaxial leaf surface (primary and secondary veins); smooth eglandular trichomes, smooth glandular trichomes, or barbellate trichomes on the branch surface nodes; and

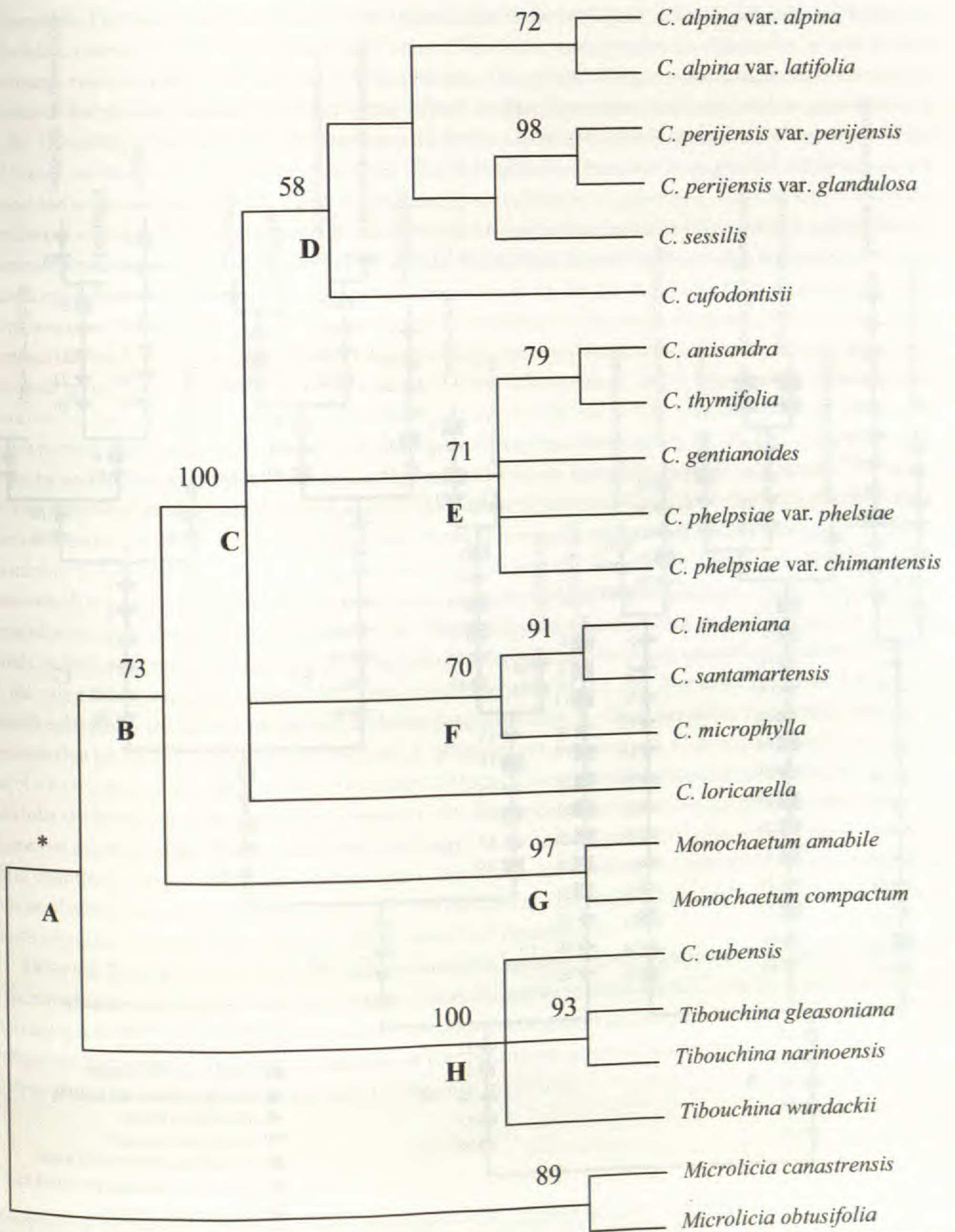


FIG. 2. Strict consensus tree generated from a branch and bound analysis of morphological characters and a backbone constraint, defining the outgroups as *Monochaetum*, *Microlicia*, *Tibouchina*, and *Chaetolepis cubensis* (analysis 2). Bootstrap values greater than 50% are shown above the branches. Letters represent the nodes above them. An "*" is used to represent the node of the backbone constraint.

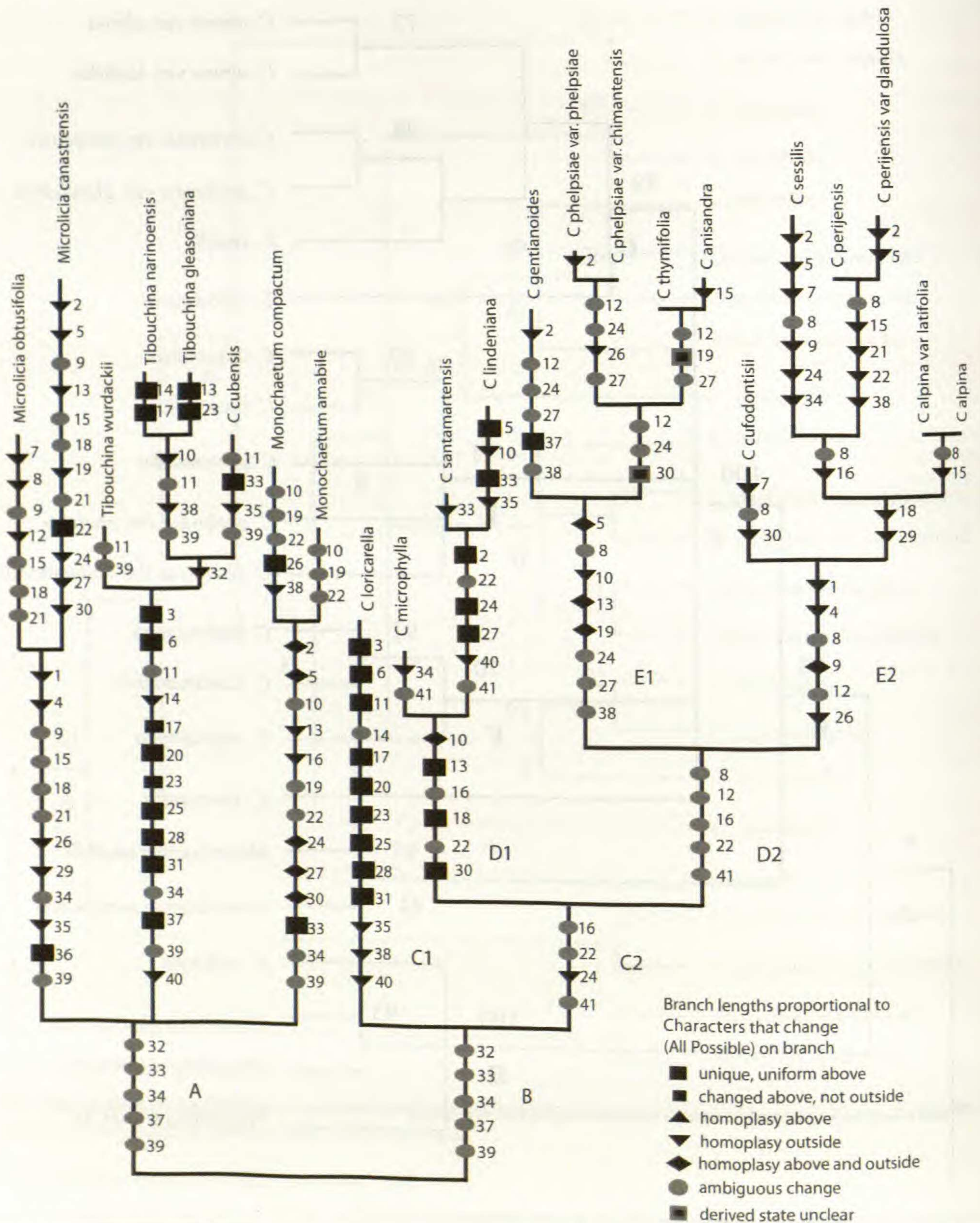


FIG. 3. One of twenty-six most parsimonious trees generated from a branch and bound analysis of the ingroup, *Chaetolepis*, and the outgroups *Microlicia*, *Monochaetum*, and *Tibouchina* (analysis 2). Character numbers are shown to the right of the hash mark. Letters A, B, C, D, and E represent nodes to the left of them.

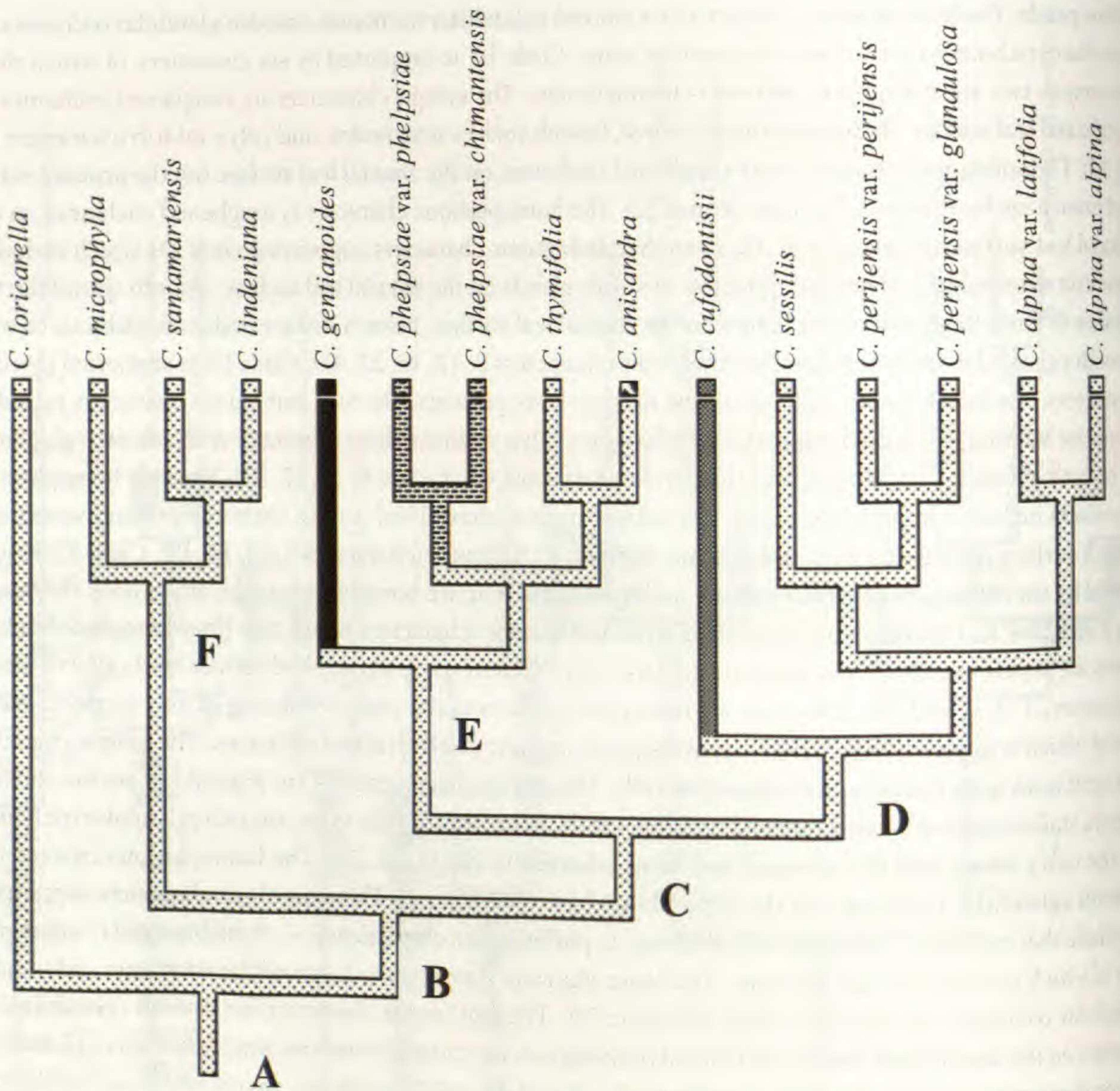
yellow petals. The homoplasious characters are smooth eglandular trichomes, smooth glandular trichomes, or barbellate trichomes on the intercalycine lobe sinus. Clade D1 is supported by six characters, of which three are unique, two are ambiguous, and one is homoplasious. The unique characters are roughened trichomes on the abaxial leaf surface (between primary veins), branch surface internodes, and calyx midrib (characters 13, 19, 30). The ambiguous characters are roughened trichomes on the abaxial leaf surface (on the primary veins) and branch surface nodes (character 16 and 22). The homoplasious character is roughened trichomes on the adaxial leaf surface (character 10). There are five ambiguous characters supporting clade D2 which include a crenulate or serrulate leaf margin, punctate or sessile glands on the abaxial leaf surface, smooth eglandular trichomes or smooth glandular trichomes on the abaxial leaf surface, branch surface nodes are glabrous or with smooth eglandular trichomes, and yellow petals (characters 8, 12, 16, 22, 41). Clade E1 is supported by eight characters, of which four are ambiguous and four are homoplasious. The four ambiguous characters include a crenulate leaf margin, forked intercalycine lobe sinus, calyx vestiture that is absent or with smooth eglandular or smooth glandular trichomes, and three to five leaf veins (characters 8, 24, 27, 38). The four homoplasious characters include a hypanthium apex, adaxial leaf surface, abaxial leaf surface (between primary veins), and branch surface internodes with smooth and eglandular trichomes (characters 5, 10, 13, 19). Clade E2 is supported by six characters of which two are ambiguous and four are homoplasious. The ambiguous characters are a serrulate leaf margin and punctate abaxial leaf surface (characters 8 and 12). The homoplasious characters are sessile glands on the hypanthium base, hypanthium apex, adaxial leaf surface, and calyx vestiture (characters 1, 4, 9, and 26). There are six characters supporting the clade consisting of only *C. gentianoides*, one of which is unique, four of which are ambiguous, and one of which is homoplasious. The unique character is a seed testa with elongate, interdigitating cells. The ambiguous characters are abaxial leaf surface lacking glands, stalked and variously branched trichomes at the intercalycine lobe sinus, smooth eglandular trichomes on the calyx lobes, and five elevated leaf veins (characters 12, 24, 27, 38). The homoplasious character is smooth eglandular trichomes on the hypanthium base (character 2). There are three characters supporting the clade that includes *C. phelpisiae* var. *phelpisiae*, *C. phelpisiae* var. *chimantensis*, *C. thymifolia*, and *C. anisandra*, one of which is an unclear derived state. This latter character state is smooth eglandular trichomes and smooth glandular trichomes on the calyx lobes (character 30). The ambiguous characters are smooth eglandular trichomes on the abaxial leaf surface and forked trichomes on the intercalycine lobe sinus (characters 12 and 24). Three characters support the clade consisting of *C. thymifolia* and *C. anisandra*, two of which are ambiguous and one of which is an unclear derived state. The two ambiguous characters are abaxial leaf surface with sessile glands (character 12) and calyx vestiture devoid of scales (character 27).

Historical Biogeography.—The first Fitch optimization analysis, which is four steps long, places the Andes at the most basal node (Fig. 4). One dispersal each from the Andes to West Africa, Costa Rica, and Venezuelan Guayana is inferred. The results of the second Fitch optimization analysis, which is nine steps long, are largely ambiguous (not shown). However, a majority of the most parsimonious reconstructions (20 of 32) of this analysis places Sierra Nevada de Santa Marta at the most basal node.

DISCUSSION

I. Cladistic Analysis

Monophyly of Traditionally Circumscribed *Chaetolepis*.—The cladistic analysis indicates that *Chaetolepis* is not monophyletic as traditionally circumscribed because *C. cubensis* is more closely related to the outgroup taxa *Tibouchina gleasoniana*, *Tibouchina narinoensis*, and *Tibouchina wurdackii* than to other congeners (Fig. 1). *Chaetolepis cubensis* and the species of *Tibouchina* in the outgroup share a tuberculate seed testa (Fig. 6 d–f) and trichomes modified into scales that are adnate to the foliar epidermis (adaxial surface) for $\frac{1}{3}$ to $\frac{2}{3}$ of their length. This species was probably transferred to *Chaetolepis* by Triana (1871) because of its four-merous flowers, markedly reduced pedoconnective and inconspicuous ventral staminal appendage. Our results, however, demonstrate that the above characters are not synapomorphies for the genus. Based on the phylogenetic results and the character differences, we propose the return of *C. cubensis* to *Tibouchina* (see Excluded Species).



Character 1 = Andes Mountains (Eastern Cordillera, Sierra Nevada de Santa Marta)
 Character 2 = Tepuis, Venezuela
 Character 3 = Talamanca Mountains, Costa Rica
 Character 4 = Loma Mountains, West Africa

Character 1 unordered

1 [dotted pattern]
 2 [horizontal lines pattern]
 3 [diagonal lines pattern]
 4 [solid black pattern]
 polymorphic [checkered pattern]

FIG. 4. A Fitch optimization using 4 areas and 1 of 26 tree topologies generated from a branch and bound search of *Chaetolepis* (analysis 2).

Likely sister outgroup of Chaetolepis when excluding C. cubensis (Chaetolepis sensu stricto).—An analysis of morphological data used in this study suggests that *Monochaetum*, not *Tibouchina* as proposed by Wurdack (1973), is likely sister to *Chaetolepis sensu stricto*. The characters that support this relationship are a dorsal orientation of the anther pore, four-merous flowers (Fig. 3). However, it cannot be ascertained from this study whether these are synapomorphies for *Chaetolepis* and *Monochaetum* or for the remainder of the outgroup. Additional similarities between *Chaetolepis* and *Monochaetum* include a four-locular ovary, cochleate seed shape, compressed/flattened cells of the seed testa, a montane habitat in tropical America, and a chromosome number based on $x = 9$ (Almeda and Chuang 1992; Solt and Wurdack 1980), although the latter two characters may ultimately be demonstrated to be symplesiomorphies for these genera.

Infrageneric relationships and character evolution.—Despite the fact that the strict consensus tree exhibited several areas of nonresolution, four major clades were resolved (clades D, E, F and *Chaetolepis loricarella* in Fig. 2). These clades are based largely on the kinds of trichomes found on various morphological organs, a character that Wurdack (1986) surmised was of phylogenetic importance among Melastomataceae. Trichome diversity in *Chaetolepis* includes scales, barbellate/dendritic trichomes, smooth eglandular trichomes or smooth glandular trichomes, and sessile glands. *Chaetolepis loricarella* is the only species in the ingroup with an indument of scales: thus this character is autapomorphic within *Chaetolepis*.

The clade comprising *Chaetolepis microphylla*, *C. santamartensis*, and *C. lindeniana* (Fig. 3, Clade D1) in the second cladistic analysis showing character state change is supported by four unambiguous characters whose character states all involve barbellate trichomes. The only other species in the analysis that has barbellate trichomes is *Monochaetum compactum* (a species within the outgroup). Thus this character state is likely to be derived within *Chaetolepis*. Similarly, the clade comprising *Chaetolepis gentianoides*, *C. phelpsiae* var. *phelpsiae*, *C. phelpsiae* var. *chimantensis*, *C. thymifolia*, and *C. anisandra* (Fig. 3, Clade E1) is supported by four unambiguous characters states that all involve smooth eglandular trichomes. The only other species in the analysis that has this character is *Monochaetum amabile*. Thus this character state is also likely to be derived within *Chaetolepis*.

—The clade comprising *Chaetolepis cufodontisii*, *C. perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. alpina* var. *alpina*, and *C. alpina* var. *latifolia* (Fig. 3, Clade E2) is supported by four unambiguous characters whose character states all involve the presence of sessile glands on the adaxial leaf surface. This is clearly a derived character state within *Chaetolepis* for these characters.

—*Chaetolepis loricarella*, *C. lindeniana*, *C. santamartensis*, and all the outgroup taxa have magenta colored petals (including *C. cubensis*), whereas all other species of *Chaetolepis* have yellow petals. Although yellow petals are ambiguously placed in the character optimizations (character 41; see Fig. 3), it is clearly derived within *Chaetolepis*. The same three *Chaetolepis* spp. *sensu stricto* have petals with ciliate margins, as do *C. cubensis* and all species of *Tibouchina*. This character is inferred to have evolved twice within *Chaetolepis*, as well as once within the outgroup, *Tibouchina*.

—*Chaetolepis gentianoides* from West Africa is the only species with elongate somewhat convex or domed periclinal walls on the seed testa (Fig. 6 g–i) but it is nested within *Chaetolepis* in the strict consensus tree of the second analysis. All other species of *Chaetolepis* have periclinal cell walls on the seed testa that are compressed/flattened and not conspicuously elongate (Figs. 5–6). The outgroup taxa have either a foveolate or tuberculate seed testa. Elongate interdigitating cells on the seed testa appear to have evolved only within *C. gentianoides* and is thus autapomorphic. An expanded survey of seed micromorphology may provide a clue to possible relationships of this species with other genera of the tribe Melastomeae in Africa.

Historical Biogeography.—The first Fitch optimization supports the eastern cordillera of the Colombian and Venezuelan Andes as the place of origin for the genus (Fig. 4). The second Fitch optimization analysis suggests an origin in the Sierra Nevada de Santa Marta, although a minority of various other equally optimal constructions of area onto the topology result in different scenarios. The Sierra Nevada de Santa Marta in northern Colombia and its nearest montane neighbor, the Sierra de Perijá (a branch of the eastern cordillera of the Colombian Andes) are distinct mountain systems with independent origins (Todd & Carriker 1922; Irving

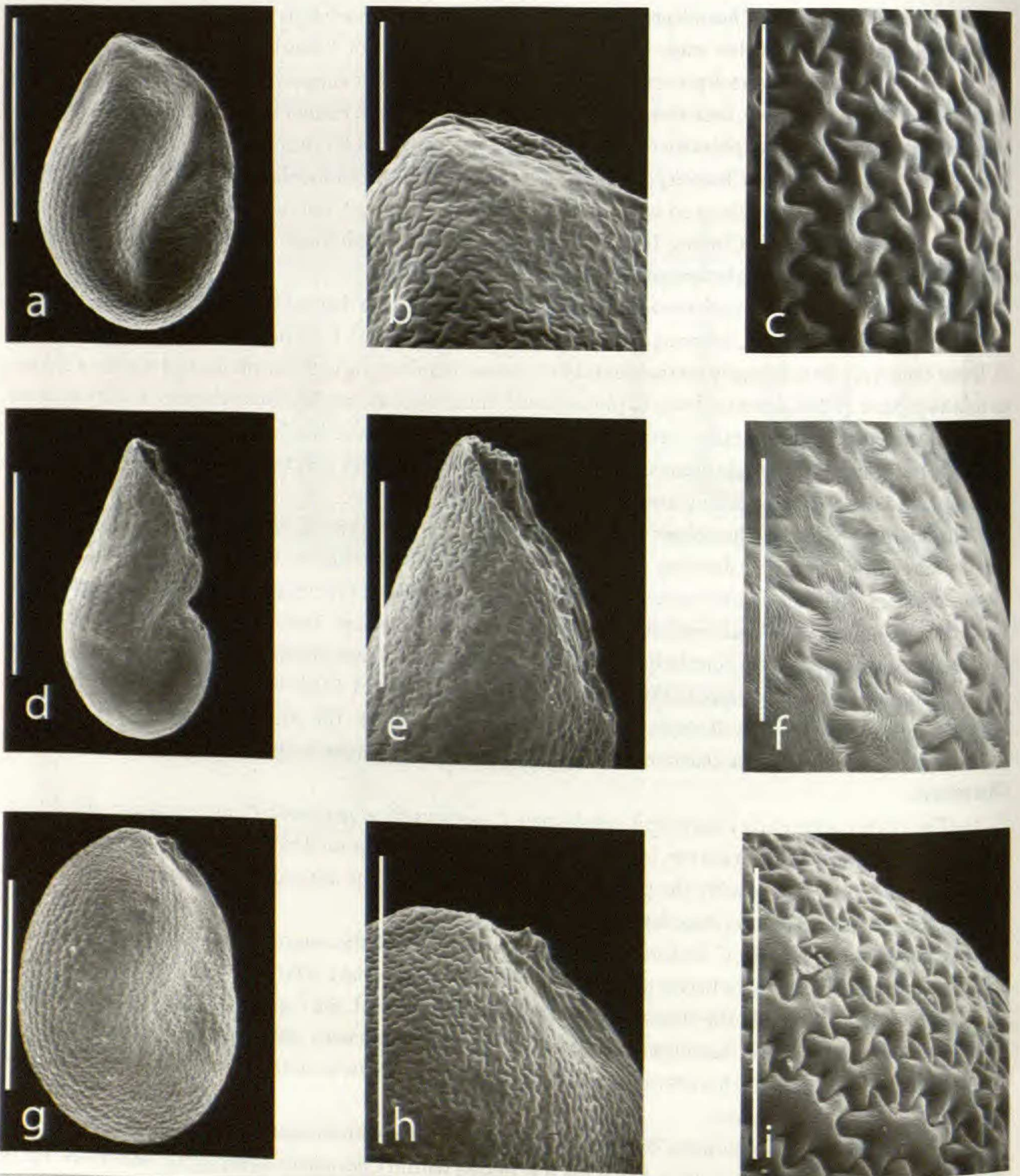


FIG. 5. Scanning electron micrographs of *Chaetolepis* seeds. **a–c.** *C. alpina* (Killip & Smith 18214): **a.** Profile view; **b.** Enlarged portion of seed coat; **c.** Enlarged portion of seed coat. **d–f.** *C. lindeniana* (Killip & Smith 19596): **d.** Profile view; **e.** Enlarged portion of seed coat; **f.** Enlarged portion of seed coat. **g–i.** *C. microphylla* (McDougal & Roldan 3640): **g.** Profile view; **h.** Enlarged portion of seed coat; **i.** Enlarged portion of seed coat. Scale bars: **a** = 0.3 μm , **b** = 0.07 μm , **c** = 0.10 μm , **d** = 0.35 μm , **e** = 0.28 μm , **f** = 0.05 μm , **g** = 0.25 μm , **h** = 0.17 μm , **i** = 0.08 μm .

1975). The Sierra Nevada de Santa Marta is the most northern and isolated land mass in northern Colombia. It has often been considered part of the Andean region (Simpson 1975; Rangel-Ch. & Garzón-C. 1997). This massif was underwater until the mid-Tertiary but its uplift began in the late Miocene and continued with substantial block-lifting in the early Pleistocene (Gansser 1955; Simpson 1975). Uplift of the eastern cordillera of Colombia and adjacent Venezuela (including the Sierra de Perijá and Mérida Andes) began in the Upper Creta-

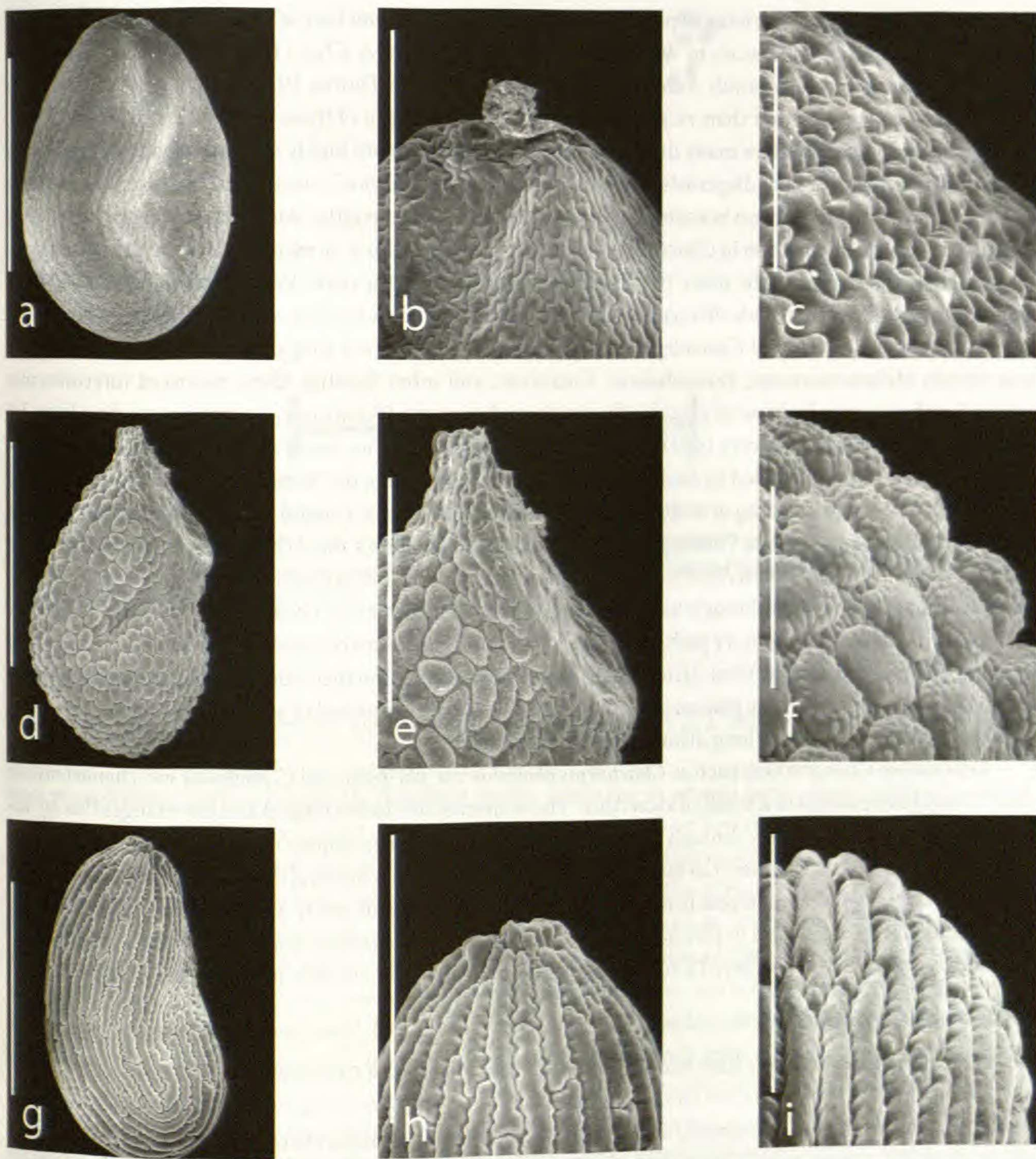


FIG. 6. Scanning electron micrographs of *Chaetolepis* seeds. **a–c.** *C. anisandra* (Tate 153): **a.** Profile view; **b.** Enlarged portion of seed coat; **c.** Enlarged portion of seed coat. **d–f.** *C. cubensis* (Killip 42939): **d.** Profile view; **e.** Enlarged portion of seed coat; **f.** Enlarged portion of seed coat. **g–j.** *C. gentianoides* (Jacques-Félix 235): **g.** Profile view; **h.** Enlarged portion of seed coat; **i.** Enlarged portion of seed coat. Scale bars: **a** = 0.3 μm , **b** = 0.07 μm , **c** = 0.10 μm , **d** = 0.35 μm , **e** = 0.28 μm , **f** = 0.05 μm , **g** = 0.25 μm , **h** = 0.17 μm , **i** = 0.08 μm .

ceous but substantial uplift above surrounding terrain was only achieved in Tertiary time beginning in the Paleocene with continued upward movement culminating in the Pliocene (van der Hammen 1961; Irving 1975; Simpson 1975).

Renner and Meyer (2001) postulated that the occurrence of *Chaetolepis gentianoides* in West Africa resulted from a long-distance dispersal event because of the "great morphological similarity between certain" South American "and West African taxa" of Melastomataceae. Our data appear to support this hypothesis. In a similar study using molecular data, Givnish et al. (2004) concluded that long-distance dispersal was also re-

sponsible for the present distribution pattern of *Pitcairnia* L' Hér. (Bromeliaceae), a genus centered in tropical America with one endemic species in West Africa [*Pitcairnia feliciana* (A. Chev.) Harms & Mildbr.]. That study postulated that many other South American-African disjuncts (see Thorne 1973; 1992) have resulted from long-distance dispersal rather than vicariance events, because the split of these two continents is too old (ca. 80 million years) to account for many disjuncts, especially those that are highly similar morphologically, such as *Chaetolepis*. The timing of dispersals to Africa from the Andes cannot be estimated because data from the present study are based only on branching patterns, and not branch lengths. An independent test of whether the amphi-Atlantic disjunction in *Chaetolepis* is due to ancient vicariance or more recent-long distance dispersal, as well as the timing of the other two dispersals inferred from the data (Venezuelan Guayana and Tamanca Range) will require clade divergence estimates based on molecular data, such as DNA sequences.

As for the distribution of *Chaetolepis* species within South America, long distance dispersal of different taxa within Melastomataceae, Bromeliaceae, Cactaceae, and other families likely occurred intermittently within South America because of climatic fluctuations during the Pleistocene, a period extending from 1.8 million to 11,550 years ago (Berry 1982). The movement of species within South America and beyond is speculative but it may have been aided by bird migration. As bird species, like the Swainson's Hawk (*Buteo swainsoni* Bonaparte), traveled to breeding or wintering grounds along the Atlantic Coastal flyway or bird species like the Arctic Tern (*Sterna paradisaea* Pontoppidan) migrated annually across the Atlantic from North America to Europe, West Africa, and South America and back they may have unintentionally picked up *Chaetolepis* seeds on their feet as they walked through mud in search of food (Lincoln et al. 1998). The Arctic Tern is the only example of a bird with a migratory path passing through both South America and Africa, but it is not known to frequent higher elevations in West Africa where *Chaetolepis* occurs. Further studies using molecular data are needed to confirm or reject the placement of *C. gentianoides* in the genus and to estimate divergence times that could assess the likelihood of long distance dispersal to Africa.

Venezuelan Guayana taxa such as *Chaetolepis phelpsiae* var. *phelpsiae* and *C. phelpsiae* var. *chimantensis* in clade E may have evolved as a result of vicariance. These species are closely related and have ranges that are adjacent to one another. Probably through time, erosion of the sandstone landmass of the tepui landscape isolated populations and led to speciation. Givnish et al. (2004) estimated that "chemical dissolution and erosion should cause the margins of adjacent tepuis to retreat from each other at a rate of nearly 2.4 km/million years. Such low rates would permit vicariance to play a role only on tepuis that are currently quite close to each other. Vicariance seems unlikely to have played a role in speciation on tepuis that are now further apart than ca. 35 km."

II. Chromosome Cytology

Meiotic chromosome numbers have been published for three species of *Chaetolepis*.

Favarger (1962) reported $n = 9$ for *C. gentianoides* (as *Nerophila gentianoides* Naudin) and Solt & Wurdack (1980) reported $n = 9$ for *C. microphylla* and $n = 18$ for *C. lindeniana*. We report here the first count for *C. cufodontisii*; $n = 9$. In this species meiosis was regular in all cells studied and all figures examined at diakinesis and telophase II were clear and consistent (Fig. 7). Present data indicate that the base number for *Chaetolepis* is $x = 9$. A base number of $x = 12$ has repeatedly been invoked as the original base number for the Melastomataceae and the order Myrtales (Raven 1975; Johnson & Briggs 1984; Graham et al. 1993; Almeda 1997a; Almeda & Robinson 2011). A base number of $x = 9$ could be derived through descending dysploidy. Thus, the three species of *Chaetolepis* with $n = 9$ have retained the base chromosome number in the genus whereas *C. lindeniana*, with $n = 18$, is clearly tetraploid based on $x = 9$. Among the significant outgroups and sister genera of *Chaetolepis*, *Bucquetia* DC. has $n = 18$ (Solt & Wurdack 1980); *Monochaetum* (DC.) Naudin has $x = 18$ (Almeda 1997b); and *Tibouchina* Aubl. has $x = 9$ (Almeda 1997b). No chromosome numbers are known for the ditypic genus *Castratella* Naudin. Of the five patterns of chromosomal evolution proposed to account for the origin and diversity of numbers for neotropical Melastomataceae (Almeda 1997b; Almeda 2013; Almeda & Chuang 1992), *Chaetolepis* appears to fit the one in which intrageneric euploidy has played a role in speciation whereas the origin of closely related genera such as *Bucquetia* and *Monochaetum* can be accounted for by paleopolyploid events.

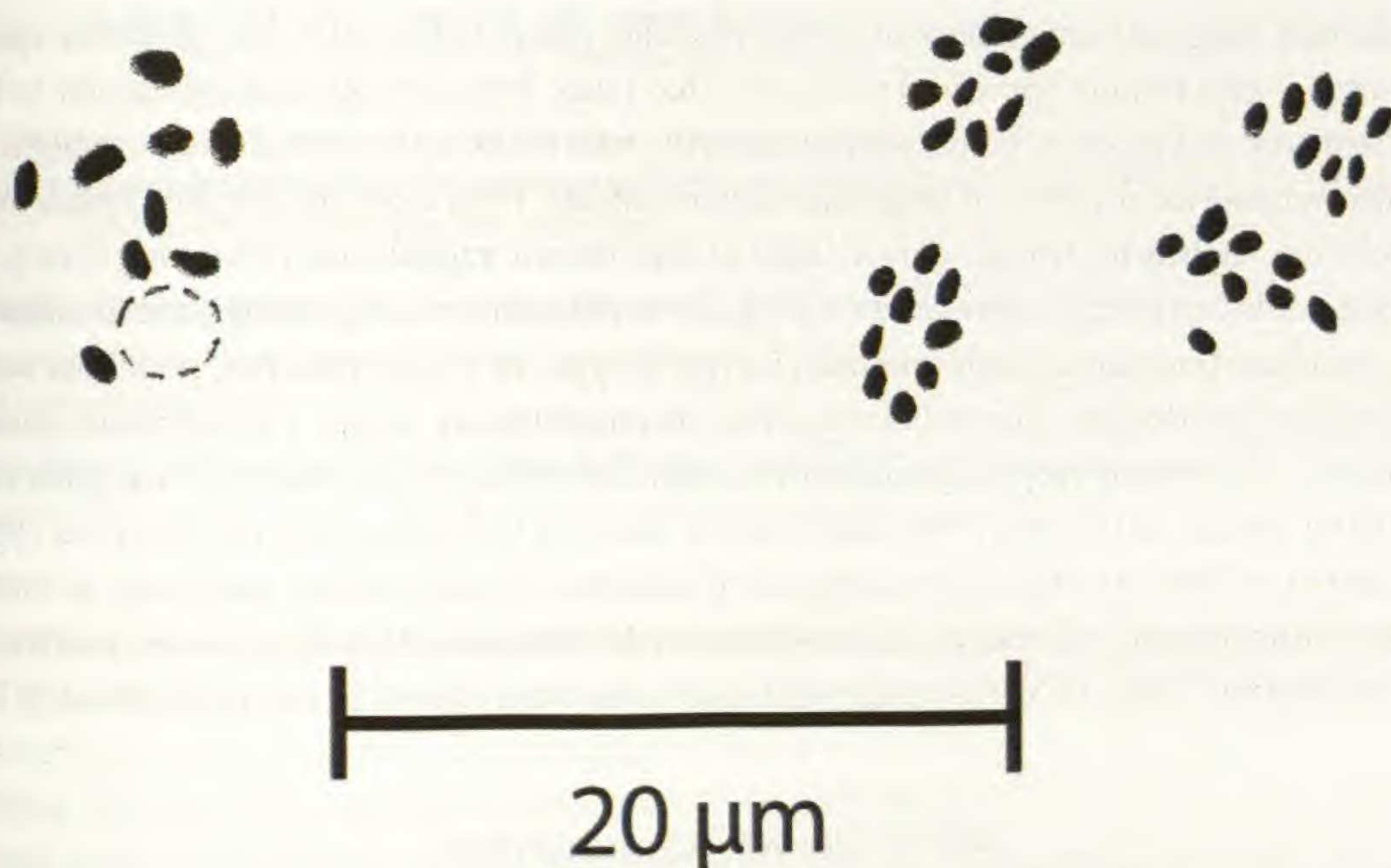


FIG. 7. Camera lucida drawings of meiotic chromosome figures of *Chaetolepis*. Meiotic stages are indicated by DIAK (diakinesis), TII (Telophase II). a. *C. cufodontisii*, $n = 9$, DIAK. b. *C. cufodontisii*, $n = 9$, TII.

III. Taxonomic Treatment

Chaetolepis Miq., Comm. Phyt. 72. 1840. *Rhexia microphylla* Bonpl., Rhex. 4, pl. 2. 1806–1808. TYPE: *Chaetolepis microphylla* (Bonpl.) Miq.

Erect or ascending, laxly or compactly branched *shrubs*, *subshrubs*, or annual *herbs*. *Distal cauline internodes* usually quadrate or subquadrate, sometimes carinate; glabrous or covered with various kinds of trichomes, scales, or glands; *distal cauline nodes* somewhat thickened, often covered with trichomes, scales, or glands like those found on the internodes but trichomes and scales when present tending to be longer. *Older internodes* terete. *Principal leaves* opposite, coriaceous or membranaceous, spreading or tightly appressed; *adaxial and abaxial leaf surfaces* glabrous and punctate with sessile glands, or sparsely to densely covered with trichomes or scales; *blades* varying in shape from linear, oblong, elliptic, lanceolate, ovate, deltoid to obovate; with (1–)3–7 elevated, nearly parallel, longitudinal primary and secondary veins all arising from the blade base or with secondary nerves arising from the midnerve above the blade base; *margins* ciliate or eciliate, entire, crenulate, or serrulate, often revolute; *blade petiolate* or less commonly sessile or subsessile. *Inflorescences* terminal (sometimes terminal on axillary branches); *flowers* solitary, paired, or in simple dichasia (sometimes in compound dichasia). *Bracts* subtending the inflorescence similar to principal leaves in size, shape, and indument, persistent or deciduous. *Bracteoles* subtending individual flowers ranging from lanceolate, ovate, rhombic, oblanceolate, to narrowly ovate, smaller in size than bracts, persistent to deciduous. *Hypanthia* (at anthesis) urceolate to campanulate, ovary free from hypanthium, calyx lobes, petals, and stamens inserted on the torus; *Hypanthia* (at maturity) similar to hypanthia at anthesis in both size and shape but the vascular ribs conspicuous or sometimes cryptic upon drying. *Calyx lobes* persistent, erect to spreading, deltoid to narrowly triangular or lance-triangular, apically acute sometimes rounded, margin fringed with smooth eglandular or glandular trichomes. *Petals* four, nearly horizontal at anthesis, obovate, yellow or magenta, entire, ciliate or rarely erose at the margins, apex varying from cuspidate to obtuse, glabrous, with or without a terminal trichome. *Stamens* 8, isomorphic, fertile; *filaments* yellow to pink or magenta when dry; *anthers* two-celled, glabrous, yellow or magenta, linear to arcuate, tapering apically to the dorsally or ventrally inclined pore, *apical pore* about 0.2 mm in diameter; *connective prolongation* (*pedoconnective*) absent to minutely prolonged below the anther thecae (< 1 mm long), lacking dorsal or ventral appendages or if present then poorly developed. Ovary superior, enveloped

by the hypanthium, ranging from globose to ovoid, 4-locular, placentation axile, base glabrous, apex sparsely to densely covered with minute appressed trichomes that range from smooth and eglandular to barbellate, with a persistent crown of erect trichomes surrounding the base of the style; style glabrous, straight or slightly curved distally, varying from yellow to magenta; stigma truncate. Fruit a dry loculicidal capsule. Seeds 0.4–1 mm long, cochleate, slightly to strongly curved, light to dark brown, raphe zone occupying $\frac{1}{5}$ to $\frac{1}{3}$ the length of the seed, testa cells (with SEM) arranged in a \pm regular to irregular interdigitating pattern; individual cells \pm elongated, anticlinal boundaries with undulate, S-type, U-type, or V-type patterns, periclinal walls \pm compressed/flattened or low-domed, microrelief smooth or inconspicuously striate. Chromosome number: $x = 9$.

Distribution.—A montane-tropical genus with a center of diversity in the Andes of Venezuela and Colombia with outlying species in the Sierra Nevada de Santa Marta of Colombia, and the Guayana Highlands of Venezuela/Guyana at 1400–4100 m. It also ranges to Costa Rica (Cordillera de Talamanca) at 2400–3600 m and West Africa from Senegal and eastern Guinea-Bissau to the Simandou Massif in Guinea, south to the Loma mountains and Mount Nimba of Sierra Leone, and east to the Man Massif in the Ivory Coast at 1700–2100 meters.

KEY TO THE SPECIES CHAETOLEPIS

1. Annual herb; periclinal walls of seed testa smooth, elongate and domelike; each intercalycine sinus with a bifurcate or trifurcate \pm flattened trichome; restricted to tropical West Africa (Senegal, Guinea Bissau, Guinea, Sierra Leone, and the Ivory Coast) _____ **4. *C. gentianoides***
1. Perennial shrub or subshrub; periclinal walls of seed testa appearing \pm smooth and flattened, if low and domelike then not conspicuously elongate; each intercalycine sinus with one or more trichomes, if branched then not conspicuously stalked; neotropical (Costa Rica, Colombia, Venezuela/Guyana).
 2. Leaf margin eciliate and lacking trichomes modified into scales.
 3. Principal leaves linear-oblong; petioles 0.5–1.5 mm; hypanthium beset with sessile glands; adaxial leaf surface punctate; primary veins on the abaxial leaf surface with smooth eglandular trichomes; cauline internodes glabrous; Costa Rica _____ **3. *C. cufodontisii***
 3. Principal leaves elliptic to oblong-elliptic, sessile; hypanthium with sessile glands and with smooth eglandular trichomes; adaxial leaf surface glabrous; primary veins on the abaxial leaf surface glabrous; cauline internodes punctate; Venezuela _____ **13. *C. sessilis***
 2. Leaf margin ciliate (the minute cilia appressed, obscure and often caducous at maturity in *C. perijensis*) or if appearing entire then fringed (at least basally) with flattened scales that have erose margins and/or an apical seta.
 4. Leaf blade with a single prominent median vein evident on the abaxial surface.
 5. Hypanthium, abaxial leaf surface, and cauline internodes covered with flattened scales; petals magenta _____ **6. *C. loricarella***
 5. Hypanthium, abaxial leaf surface, and cauline internodes with a varied indument but lacking flattened scales; petals yellow.
 6. Hypanthium with a uniform distribution of sessile glands _____ **8. *C. perijensis* var. *perijensis***
 6. Hypanthium with a uniformly distributed mixture of sessile glands and stalked glandular trichomes _____ **9. *C. perijensis* var. *glandulosa***
4. Leaf blade with three or more prominent veins evident on the abaxial surface.
 7. Petals magenta or lilac-violet, the margins ciliate.
 8. Principal leaves 3-nerved; adaxial leaf surface with bulla based trichomes; pedicels 2–5 mm long; calyx lobes 0.8–1 mm wide, acute apically _____ **5. *C. lindeniana***
 8. Principal leaves 5–7-plinerved; adaxial leaf surface with minutely barbellate trichomes; pedicels 1–2 mm long; calyx lobes 2.5–3 mm wide, rounded apically _____ **12. *C. santamartensis***
 7. Petals yellow, the margins eciliate.
 9. Leaf margin entire; adaxial leaf surface, abaxial leaf surface, and cauline internodes covered with barbellate or dendritic trichomes with short or well-developed axes and a moderate number of short terete arms _____ **7. *C. microphylla***
 9. Leaf margin crenulate; adaxial leaf surface, abaxial leaf surface, and cauline internodes not covered with barbellate or dendritic trichomes.
 10. Base of hypanthium with smooth eglandular trichomes _____ **10. *C. phelpsiae* var. *phelpsiae***
 10. Base of hypanthium glabrous or with sessile glands.
 11. Cauline internodes with smooth eglandular and smooth gland-tipped trichomes; primary and secondary veins on abaxial leaf surface variously beset with sessile glands and/or smooth gland-tipped and smooth eglandular trichomes; distal portion of hypanthium around the torus with smooth eglandular trichomes.
 12. Abaxial leaf surface covered with sessile glands and smooth eglandular trichomes; calyx lobes midrib with smooth eglandular trichomes, otherwise glabrous _____ **2. *C. anisandra***

12. Abaxial leaf surface punctate with smooth, eglandular trichomes and smooth gland-tipped trichomes; calyx lobes beset with sessile glands, stalked glandular and eglandular trichomes both on and off the midrib _____ **11. *C. phelpsiae* var. *chimantensis***
11. Cauline internodes with sessile glands or sometimes replaced by smooth gland-tipped trichomes; primary and secondary veins on abaxial leaf surface glabrous; distal portion of hypanthium around the torus lacking smooth eglandular trichomes _____ **1. *C. alpina***

1. *Chaetolepis alpina* Naudin, Ann. Sci. Nat. Bot. sér. 3, 14:140. 1850. (Figs. 5 a–c; 8). TYPE: COLOMBIA: PROVINCE OF PAMPLONA: at 3000–3200 m, *Linden 724* (LECTOTYPE, designated by Martin & Cremers 2007: P!; ISOLECTOTYPES: BM!, BR! [2], F!, G!, K!, MPU, internet image, NY!).

Chaetolepis alpina var. *latifolia* Cogn., Monogr. Phan. 7:170. 1891. TYPE: VENEZUELA. PROVINCE OF CARACAS: *Funck 277* (LECTOTYPE, here designated: BR!; ISOLECTOTYPE: G!). The other syntype cited in the protologue, *Funck 484*, purportedly deposited at BR, was not seen.

Erect, compactly branched subshrub to 40 cm tall. Distal cauline internodes quadrate, winged, sparsely to moderately covered with sessile glands or sometimes intermixed with antrorsely spreading smooth eglandular trichomes. Distal cauline nodes like internodes except moderately covered with sessile glands intermixed with a sparse to moderate covering of smooth eglandular trichomes 1.5–2 mm long. Older internodes terete, woody and exfoliating with age. Principal leaves coriaceous, somewhat unequal in size in each pair; adaxially moderately covered with sessile glands; abaxially moderately punctate between primary and secondary veins, sparsely to moderately covered with smooth eglandular trichomes and sparsely to moderately covered with sessile glands on the elevated nerves or sometimes glabrous and without glands. Blades 8–13(16) × 2–3.5 mm, lanceolate, elliptic-lanceolate to lanceolate-ovate, acute to rounded apically, acute basally, the three prominent nerves extending the entire length of the blade; margins ciliate-serrulate; petioles 1–1.5 × 0.25–0.5 mm, moderately to densely covered with sessile glands. Inflorescence a simple to compound dichasium. Bracteoles 4–7 × 1–2(–3) mm, similar to principal leaves; margins ciliate-crenulate. Floral pedicels 0.8–1.2 mm long, glabrous. Hypanthia (at anthesis) 2.5–3.5 × 2–3 mm, urceolate or narrowly campanulate, yellow to magenta when dry, moderately covered with sessile glands; hypanthia (at maturity) with vascular ribs often conspicuous when dry. Calyx lobes 1.5–2 × 1–1.5 mm, erect to ascending, sometimes spreading to reflexed, deltoid to lance-triangular when dry, apically acute, ciliate, moderately covered with sessile glands; calyx moderately covered with sessile glands, sometimes with a smooth eglandular trichome on the midrib; intercalycine sinus with a smooth eglandular trichome, sometimes with a forked trichome. Petals 6–7 × 3–3.5 mm, yellow, apex cuspidate with a terminal trichome, margins entire, glabrous. Filaments 5–6 mm long, yellow; anthers 2.5–3 × 0.4–0.6 mm, yellow, linear; pore dorsally inclined; connective not prolonged below the thecae. Ovary sparsely or sometimes moderately covered with smooth eglandular trichomes; style 8–11 mm long, yellow. Seeds 0.5–0.6 mm long, brownish. Chromosome number: unknown.

Flowering.—Throughout the year.

Habitat and Distribution (Fig. 9).—Endemic to the Eastern Cordillera of Colombia in the departments of La Guajira, Santander, and Norte de Santander and the Sierra Nevada de Santa Marta in the departments of César and Magdalena at 1700–4100 meters. Found in subpáramos and páramos on rocky hillsides and cliffs.

Discussion.—*Chaetolepis alpina* is a laxly to compactly branched subshrub that is easily recognized by its sessile glands on adaxial foliar surfaces, cauline internodes, hypanthia, and calyx lobes. Other diagnostic characters include small lanceolate leaf blades that are 3-nerved; leaf margins that are ciliate-crenulate; an abaxial leaf surface that is punctate between the primary and secondary veins; and elevated veins that are covered with sessile glands and smooth eglandular trichomes.

Chaetolepis alpina is most similar to *C. perijensis*. Both species have sessile glands on their foliar surfaces, ciliate leaf margins, and punctate abaxial leaf surfaces between the primary and secondary veins. These two species also have smooth eglandular trichomes at the intercalycine sinuses; anthers with a pore that is dorsally inclined; and a seed testa that has compressed/flattened interdigitating cells. *Chaetolepis perijensis* differs from *C. alpina* by its sessile glands on cauline nodes, uninerved leaf blades with entire margins, and punctate abaxial leaf surfaces.

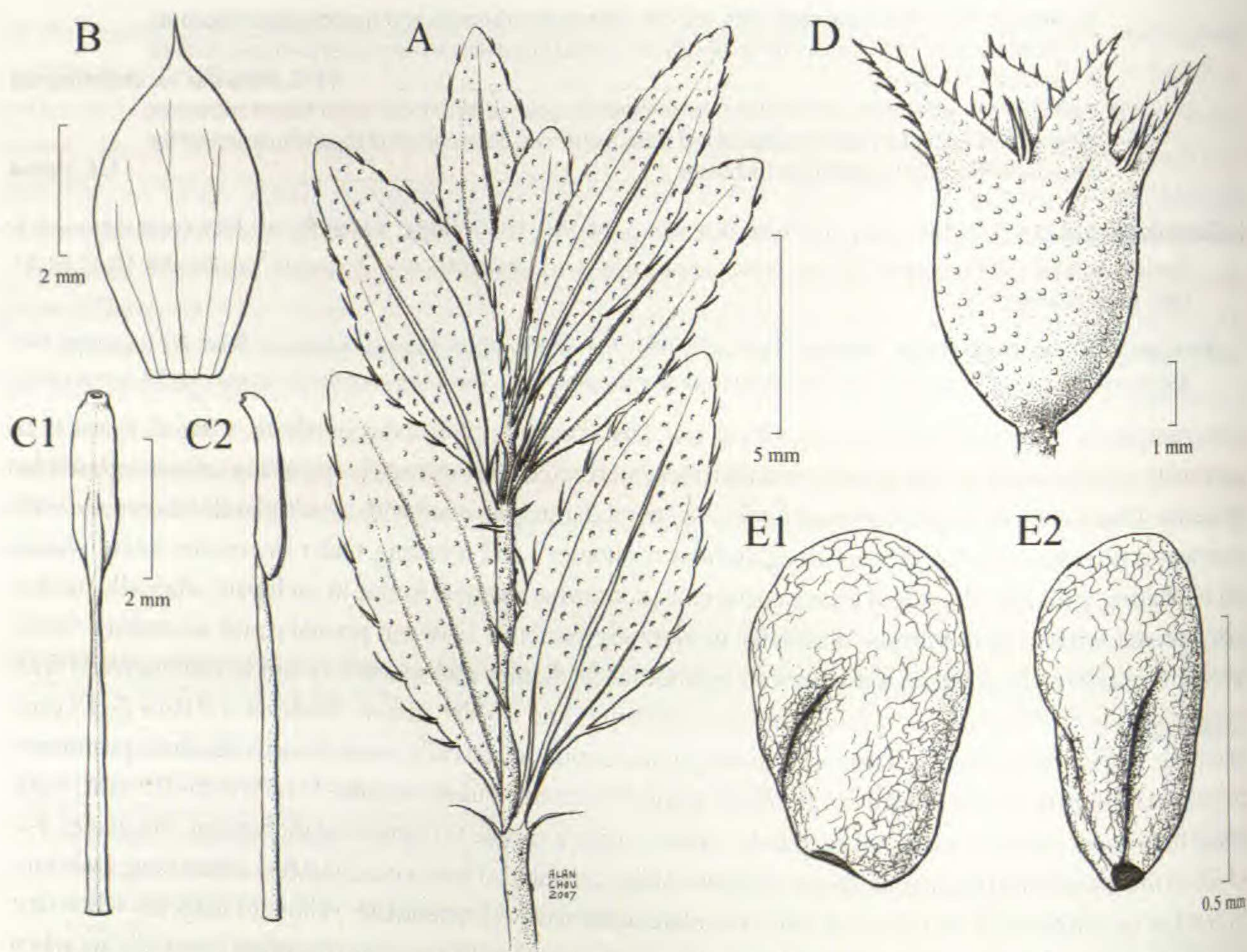


FIG. 8. *Chaetolepis alpina*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Cuadros & Gentry 2989, US).

Chaetolepis alpina has been divided into two varieties, the nominate one and *C. alpina* var. *latifolia*. According to Cogniaux (1891) the nominate variety has oblong leaves 10–15 × 3–5 mm and var. *latifolia* has ovate leaves 8–13 × 4–8 mm. After study of many more collections than were available to Cogniaux, we could not detect non-overlapping morphological differences between the two. One collection, Smith 768, that was identified as *C. alpina* var. *latifolia* differed by its lack of foliar glands and presence of eglandular trichomes on the cauline internodes. In all other respects it is readily accommodated within *C. alpina*.

Additional specimens examined: **COLOMBIA. César:** Municipio Pueblo Bello, Nabusimake, Stancik 190 (COL). **Norte de Santander:** Prov. de Pamplona, La Baja, Funck & Schlim 1313 (BR). **La Guajira:** Riohacha, Macotama, Sierra Nevada de Santa Marta, Carbonó 710 (UTMC); Sierra Nevada de Santa Marta, Vertiente Río San Miguel, Cuadros & Gentry 2735 (MO); Serranía de Perijá, Cerro Pintado, Cuadros & Gentry 3501 (MO). **Magdalena:** Sierra Nevada de Santa Marta, entre San Pedro y cabeceras del Río Sevilla, Barclay & Juajibioy 6799 (COL, MO); Sierra Nevada de Santa Marta, Cerro Kennedy, Cuadros & Gentry 2989 (US); Sierra Nevada de Santa Marta, se slopes, Hoya del Río Donachuí, Cuatrecasas & Castaneda 24667 (NY); Sierra Nevada de Santa Marta, se slopes, Hoya del Río Donachuí, Cuatrecasas & Castaneda 24857 (COL); Sierra Nevada de Santa Marta, camino entre quebrada Cebolleta y San Pedro, extremo oriental de la Cuchilla Yerbabuena, Forero & Kirkbride 669 (COL, MO, NY, US); Sierra Nevada de Santa Marta, in San Sebastian de la Sierra, Funck 484 (BM, BR, K); Sierra Nevada de Santa Marta, entre Canguruaca y Corisa, van der Hammen 1136 (COL); Sierra Nevada de Santa Marta, Caserío de San Sebastian, Rangel & Sturm 1863 (NY); Valledupar, San Sebastian de Rabago, Romero-Castaneda 907 (COL); Sierra Nevada de Santa Marta, ca. 30 mi inland from Dibulla, Seifriz 441 (NY); Sierra Nevada de Santa Marta, Smith 768 (BR [2]); vicinity of two small lakes near source of Río Yebosimeina, White & Alverplona, por Garcia (sur de ciudad), Fabrega 986 (F); Cucutilla, Páramo El Romeral, Ortiz et al. NYO122 (COL). **Santander:** edge of Páramo de Santurbán, near Vetas, Killip & Smith 17589 (F, GH, NY); vicinity of Vetas, Killip & Smith 17901 (NY); Páramo de las Puentes, above La Baja, Killip & Smith 18214 (GH, NY); Páramo de las Puentes, above La Baja, Killip & Smith 18227 (NY); Páramo de las Coloradas, above La Baja, Killip & Smith 18434 (NY); Ibid., Killip & Smith 18467 (F, GH, NY, P); Páramo de Romeral, Killip & Smith 18565 (BM, GH, MO, NY); western

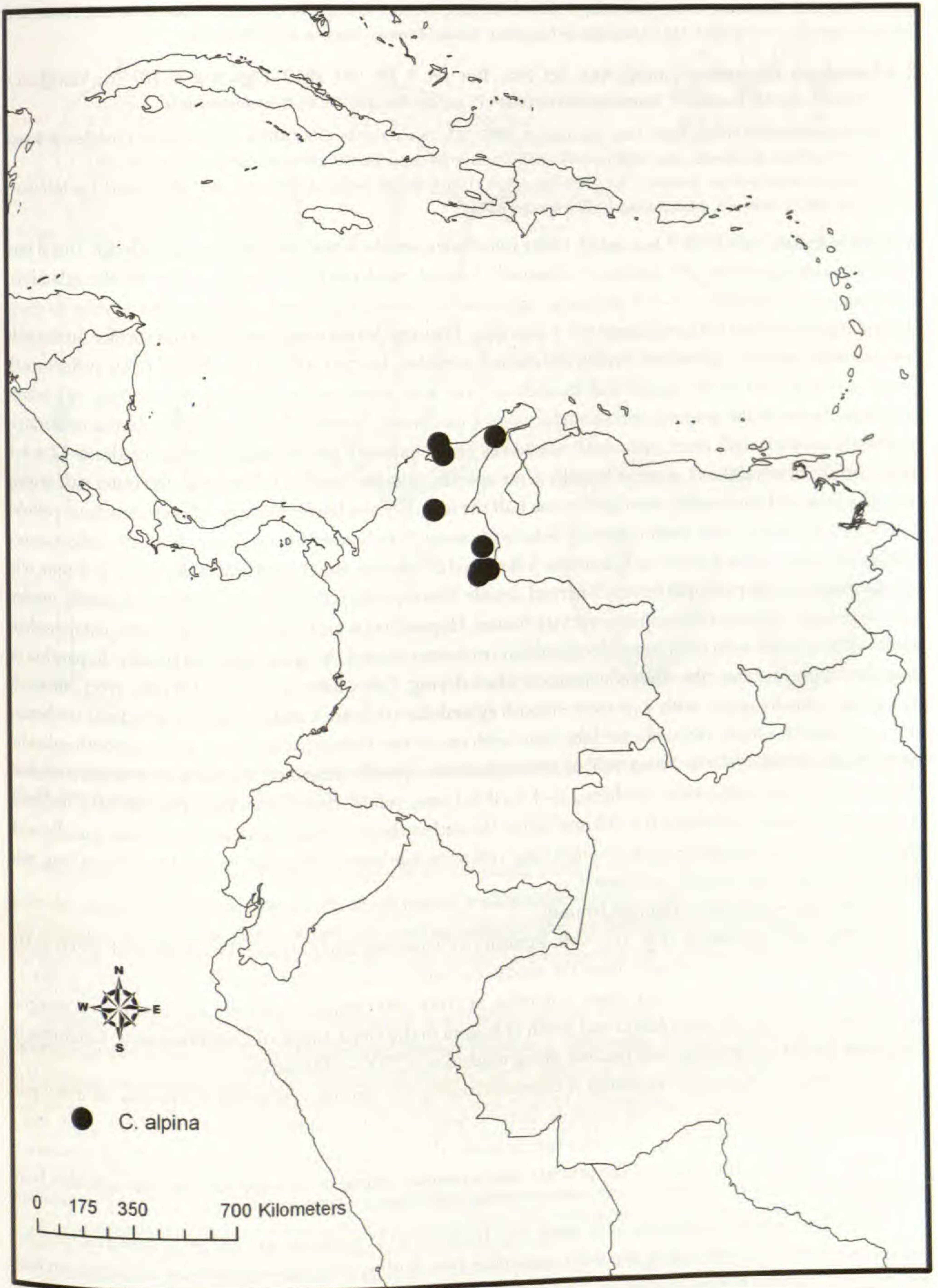


FIG. 9. Distribution of *Chaetolepis alpina*.

slope of Páramo de Santurbán, toward Tona, Killip & Smith 19532 (GH, NY, US); Municipio de Cucutilla, Vereda El Carrizal, Páramo de El Romeral, Sánchez et al. 5138 (HECASA); Municipio de Pamplona, Vereda El Volcán, Solano et al. 35 (HECASA).

2. *Chaetolepis anisandra* Naudin, Ann. Sci. Nat., Bot. sér. 3, 14: 140. 1850 (Figs. 6 a–c; 10). TYPE: VENEZUELA. BOLIVAR: near Mt. Roraima, R. Schomburgk 663 (HOLOTYPE: P!; ISOTYPES: BM!, BR!, G!, K!, P, internet image!).

Chaetolepis thymifolia Triana, Trans. Linn. Soc. London 28:50. 1871. Syn. nov. TYPE: COLOMBIA. CUNDINAMARCA: Cordillera de Bogotá, in the Páramo de Choachi, elev. 3400 m, 1851–1857, Triana 36178 (HOLOTYPE: BM, photo of holotype, F!; ISOTYPE: P!).

Chaetolepis citrina Gleason, Brittonia 3:174. 1939. TYPE: VENEZUELA. BOLIVAR: Mount Auyan-tepui, elev. 2200 m, G.H. Tate 1157 (HOLOTYPE: NY!; ISOTYPES: US, internet image!, VEN, internet image!).

A much branched subshrub 0.1–1 m tall. Older internodes woody, terete and exfoliating with age. Distal cauline internodes quadrate and carinate to narrowly winged, moderately to densely scabrous, the eglandular and glandular trichomes 0.4–0.5 mm long, appressed to ascending. Distal cauline nodes similar to distal cauline internodes but with trichomes 0.7–1 mm long. Principal leaves coriaceous, adaxial surface moderately covered with smooth, eglandular, evenly distributed spreading to erect trichomes; abaxial foliar surface moderately covered with sessile glands and sparsely covered with appressed or sometimes spreading, eglandular trichomes between the primary and secondary veins; moderately covered with sessile glands and moderately to densely covered with erect, eglandular trichomes on the primary and secondary veins; blades 6–12 × 4–9 mm, ovate to nearly deltoid, acute to broadly acute apically, cuneate basally, 3–5-nerved, the outer pair arising from the base and continuing one third or one half the length of the blade, margins ciliate-crenulate; petioles 2–4 × 0.25–0.5 mm, ciliate and/or sparsely beset with smooth trichomes but varying to glabrate. Inflorescence terminal, flowers solitary or borne in a simple 3-flowered dichasium. Bracts and bracteoles 5–9 × 3–6 mm, otherwise similar to the principal leaves, 3-nerved, sessile. Floral pedicels 0.5–1.0 mm long, or subsessile, moderately to densely covered with minute, erect trichomes. Hypanthia (at anthesis) 3–4.5 × 2–3 mm, campanulate, moderately covered with erect, smooth eglandular trichomes toward the apex, glabrous basally; hypanthia (at maturity) with vascular ribs often conspicuous when drying. Calyx lobes 2–2.5 × 1–1.5 mm, erect, narrowly triangular, apically acute, with 1 or more smooth eglandular trichomes and/or smooth glandular trichomes along the midrib, ciliate. Intercalyne lobe sinus with one or two forked trichomes or with a smooth eglandular trichome. Petals 7–9 × 4–5 mm, yellow, entire, glabrous, apically cuspidate, tipped with a single trichome. Filaments 3–9 mm long, yellow, anthers 2.5–4.5 × 0.5–1 mm, yellow, linear to arcuate, pore dorsally inclined; connective minutely prolonged 0.1–0.3 mm below the anther thecae. Ovary moderately covered apically with smooth eglandular trichomes. Style 6–7 mm long, yellow or pale brown when dry. Seeds 0.4–0.6 mm long, pale brown. Chromosome number: unknown.

Flowering.—September through January.

Habitat and Distribution (Fig. 11).—Mt. Roraima in Venezuela and Guyana (Wurdack et al. 1993) to Mt. Auyan-Tepui in Bolívar, Venezuela, from the sandstone bluffs to the summit at 1950–2600 meters. It also occurs on the Sierra de Perijá in Magdalena, Colombia, at 2700–2800 meters in páramo and cloud forest margins on the Sierra Nevada de Santa Marta and south of Bogotá in the Department of Cundinamarca, Colombia, in temperate forests, subpáramo, and páramo, along roadsides at 2500–3400 meters.

Discussion.—*Chaetolepis anisandra* is characterized by the smooth eglandular trichomes on distal portions of the hypanthium, both leaf surfaces, cauline nodes and internodes, and midrib of the calyx; and a glabrous hypanthium base (Fig. 10). The ovate to nearly deltoid leaf blades and sessile glands on the abaxial leaf surface (both on and between the primary and secondary veins) of this species also distinguish it from congeners.

Chaetolepis anisandra appears to be most closely related to *C. phelpsi* var. *phelpsi* based on morphological similarities as reflected in the strict consensus tree. Both species have eglandular trichomes on both leaf surfaces, cauline nodes, internodes, and midrib of the calyx lobes. Furthermore, these species both have ciliate-crenulate leaf margins, a leaf blade that is basally cuneate and 3-nerved, forked trichomes at the intercalary lobe sinuses; inappendiculate anther connectives, and a dorsally inclined anther pore.

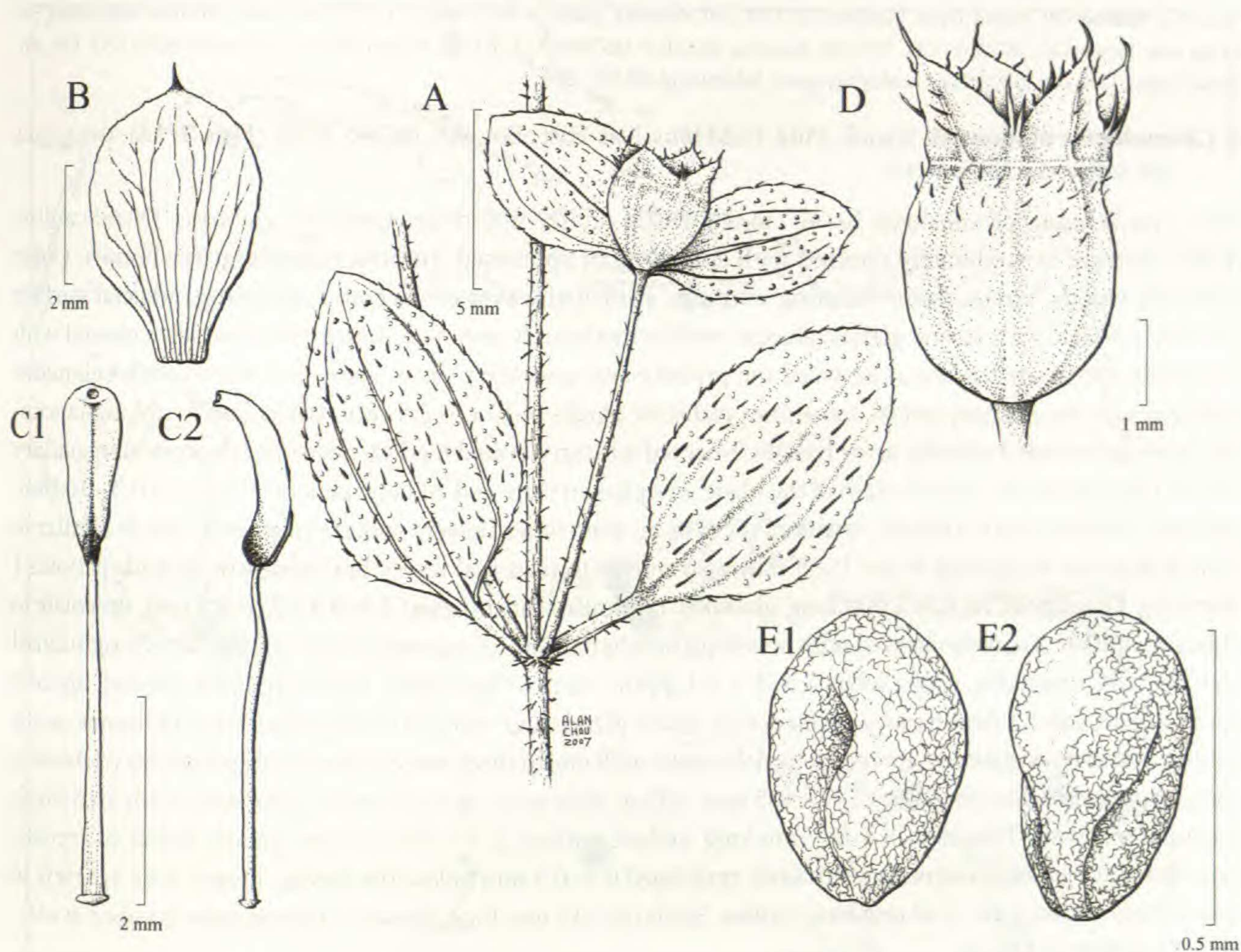


FIG. 10. *Chaetolepis anisandra*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Cardona 2720, NY).

Chaetolepis phelpsi var. *phelpsi* differs from *C. anisandra* in having smooth eglandular trichomes that cover the entire hypanthium not just the distal region, an abaxial leaf surface that is punctate with eglandular and glandular trichomes between the primary and secondary veins, an abaxial leaf surface that has eglandular and glandular trichomes on the elevated veins, and cauline internodes that are sparsely covered with eglandular and glandular trichomes (Fig. 22).

Chaetolepis thymifolia has been recognized as a distinct species based on 3-nerved leaves and ovate to suborbicular petals (vs. 3–5-nerved leaves and obovate petals in *C. anisandra*). Because the petals of all species in the genus are obovate and foliar venation is consistently 3–5-nerved in *C. anisandra*, we see no reason to continue to recognize *C. thymifolia*. What has been recognized as *C. thymifolia* occurs in central Colombia at 2500–3400 m whereas *C. anisandra* has traditionally been accorded a range extending from northern Colombia to southeastern Venezuela at 1950–2800 m.

Representative specimens examined: **COLOMBIA. César:** Valledupar, páramo bajo entre Mamancana y Nabusimake, Carbonó 3654 (UTMC). **Cundinamarca:** El Portachuelo between Une and Fosca, Cordillera Oriental vert. Oriental, en el mismo Boqueron, Cuatrecasas & Jaramillo 28795 (US); Taguate Valley, 3 km W of Gutierrez, 45 km S of Bogotá, Grant 9651 (NY, US); Páramo de Chipaque, Karsten, s.n. (BR, NY). **La Guajira:** Sierra de Perijá, E of Manaure, Cuatrecasas & Castaneda 25164 (COL, F). **Magdalena:** Municipio de Santa Marta, Corregimiento de Minca, Sierra Nevada de Santa Marta, Cuchilla de San Lorenzo, road to Cerro Kennedy, Almeda et al. 10152 (CAS, COL); Municipio de Santa Marta, Corregimiento de Minca, Sierra Nevada de Santa Marta, Cuchilla de San Lorenzo, Reserva Natural de Aves El Dorado, trail between Sendero Mirador and Sendero Quetzal Dorado, Almeda et al. 10167 (CAS, COL); Municipio de Santa Marta, Sierra Nevada de Santa Marta, Estación San Lorenzo, Carbonó 982 (CAS, UTMC). **VENEZUELA. Amazonas:** Serranía del Yutaje, Río Manapiare, Maguire

35322 (G). **Bolivar:** Mt. Auyan-Tepui, *Cardona* 2720 (NY); Mt. Roraima, *Quelch & McConnell* 22 (K); Mt. Roraima, ascent of ledge along SW facing side, *Steyermark* 58735 (F, GH, NY); Mt. Roraima, *Quelch & McConnell* 22 (K); Mt. Auyan-Tepui, *Steyermark* 94072 (NY, US); Mt. Auyan-Tepui, *G.H. Tate* 1157 (NY). Locality not given, *Schomburgk* 1013 (F, GH).

3. *Chaetolepis cufodontisii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18:792. 1938. (Figs. 7, 12). TYPE: COSTA RICA: *Endres s.n.* (HOLOTYPE: F!).

Erect, much-branched subshrub 10–40 cm tall. Distal cauline internodes quadrate, glabrous. Distal cauline nodes sparsely to moderately covered with spreading or appressed, smooth eglandular trichomes. Older branches woody, terete, and exfoliating with age. Principal leaves coriaceous, spreading, adaxial surface sparsely covered with sessile glands; abaxial surface moderately punctate, sometimes sparsely covered with antrorsely spreading trichomes between the primary and secondary veins, sparsely covered with eglandular trichomes on the primary nerve, sometimes glabrous; blades 6–10 × 1–2.5 mm, lanceolate to oblong-lanceolate, acute to rounded apically, acute basally, 3-nerved with an elevated median nerve and depressed secondary nerves that extend the entire length of the blade; margin serrulate and eciliate; petioles 0.5–1.5 × 0.3–0.5 mm, glabrous. Inflorescence a simple, terminal dichasium, sometimes flowers solitary or paired. Bracts similar to principal leaves. Bracteoles 4–6 × 1–1.5 mm, also similar to principal leaves but subsessile or with petioles 1 mm long. Floral pedicels 0.5–2 mm long, glabrous. Hypanthia (at anthesis) 3.5–4.5 × 2.5–3.5 mm, urceolate to subcampanulate, sparsely covered with sessile glands; hypanthia (at maturity) with conspicuous longitudinal vascular ribs when dry. Calyx lobes 2.5–4 × 1–1.5 mm, erect to ascending, narrowly lance-deltoid, apically acute, ciliate; calyx lobes sparsely covered with sessile glands and with antrorsely spreading trichomes on the midrib, sometimes glabrous; intercalycine lobe sinus with one to three smooth flattened eglandular trichomes, these sometimes bifurcate. Petals 5–7 × 4–5 mm, yellow, apex acute, margin entire, glabrous except for a single terminal trichome. Filaments 4.5–5.5 mm long, yellow; anthers 2–3 × 0.4–0.6 mm, yellow, linear to arcuate; pore dorsally inclined; connective minutely prolonged 0.2–0.3 mm below the thecae. Ovary apex sparsely to moderately setose; style 9–10 mm long, yellow. Seeds 0.6–0.7 mm long, brown. Chromosome number: $n = 9$.

Flowering.—All year.

Habitat and Distribution (Fig. 11).—Endemic to Costa Rica in San José and Cartago provinces on the Cordillera de Talamanca in páramo on exposed slopes with shrubby vegetation at 2400–3600 m.

Discussion.—*Chaetolepis cufodontisii* is a much-branched subshrub readily recognized by the following characters: adaxial leaf surface and hypanthium covered with sessile glands; abaxial leaf surface punctate between the primary and secondary veins with a few eglandular trichomes on the elevated veins (Fig. 12); leaves with serrulate margins; glabrous cauline internodes; and dorsally inclined anther pores.

Chaetolepis cufodontisii most closely resembles *C. alpina* of Colombia. Both species have eglandular trichomes on the cauline nodes, an adaxial leaf surface covered with sessile glands, eglandular trichomes between the primary veins, and leaf blades that are 3-nerved. In addition these two species have hypanthia covered with sessile glands, smooth eglandular trichomes on the intercalycine sinuses, and anthers with dorsally inclined pores.

Chaetolepis alpina differs from *C. cufodontisii* by its ciliate-crenulate leaf margins, and sessile glands on the primary veins of abaxial leaf surfaces, cauline internodes, and calyx lobes.

Chaetolepis cufodontisii is also superficially similar to *C. sessilis* (Fig. 24). For major differences between these two species see the key to species.

Additional specimens examined: **COSTA RICA. Cartago:** Cordillera Talamanca, near Cerro de la Muerte, *Allen* 5410 (F, G, NY, US); 1300 ft above highest point on highway, Cerro de la Muerte, Talamanca range, *Carlson* 3526 (F, NY); Cerro de las Vueltas along the Pan American highway ca. 90 km S of Cartago, *Cronquist & Muños* 8851 (NY); Cordillera de Talamanca, Asunción summit, Cerro de la Muerte, *Davidse & Pohl* 1138 (CAS, MO); Páramo de Asunción, *Gomez et al.* 2164 (MO); Cerro de la Muerte, Pan-American Highway, 5 km above Villa Mills and ca. 8 km above Nivel, *Holm & Iltis* 556 (BM, DS, F, G, K, NY, P); Cerro Sákira, Macizo Buena, *Sánchez et al.* 1398 (F, K); Cerro de la Muerte, Talamanca range, high point along Pan American highway, *Taylor* 11758 (NY); slopes of Cerro Sákira at La Asunción along the Carretera Interamericana at km 91, *Wilbur & Stone* 10043 (DUKE, F, US). **Heredia:** Zurquí [locality probably in error-unlikely it would be collected here] *Valerio* 1205 (F). **Limón:** Cordillera de Talamanca, Atlantic slope, Cerros Tararia (locally known as Tres Picos), *Grayum et al.* 28888 (CAS, MO). **San José:** Cerro Buenavista, ca. 10 km NW of the La Georgina Restaurant, en route to San José, area, *Almeda et al.* 2349 (DUKE).



FIG. 11. Distributions of *Chaetolepis anisandra* and *C. cufodontisii*.

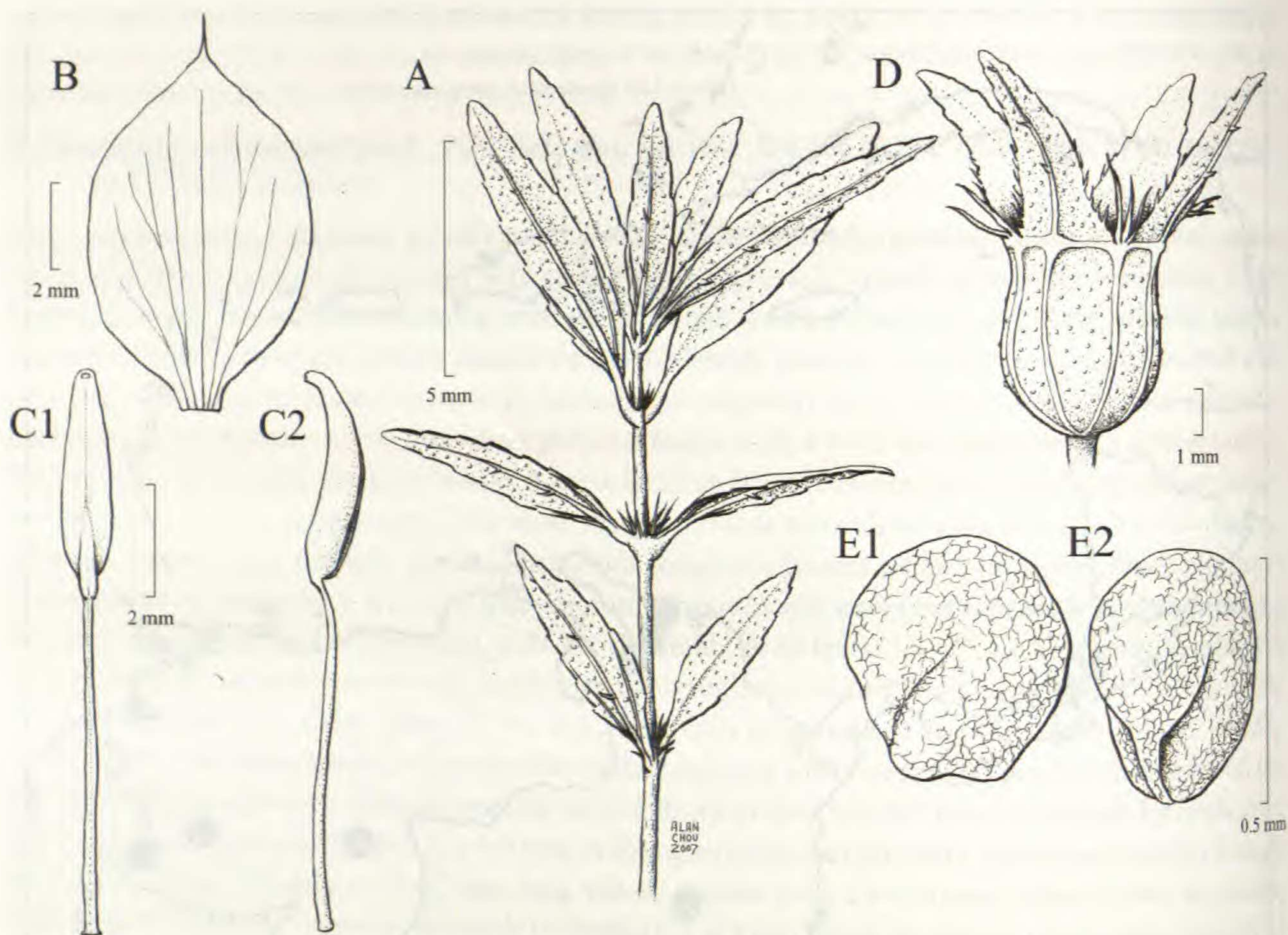


FIG. 12. *Chaetolepis cufodontisii*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Almeda & Wilbur 1605, F).

F); Cordillera de Talamanca, Vicinity of Cerro de la Muerte, Allen 5410 (NY); direct line from Hotel La Georgina to Cerro Frío of the Cerro Buenavista complex (Cerro de la Muerte), area with television and radio towers, Davidse 24987 (CAS, MO); Dos Burros, Cerro de la Muerte, Dayton 3059 (F, MO); Buena Vista, Jiménez 2662 (F); enroute to Cerro Chirripó from Canaan and on Pico Sudeste, Weston 3652 (CAS); Buena Vista, Jiménez 2663 (BM, NY); Pico Asunción, Jiménez 3382 (F); Cantón Pérez Zeledán, Parque Nacional Chirripó, Valle de Los Conejos, trail to Cerro Chirripó, Luteyn & Chaverri 15419 (CAS, NY); Páramo de Abejónal, Pittier 7823 (BR[3], G); along Interamerican highway ca. 25 km SW of road to La Cima and 4.1 km NW of Cerro Asunción, E end of abandoned section of road, Stevens 14298 (BM, CAS, F); Copey, Tonduz 11903 (F); Los Frailes, Valerio 1373 (BR, F); Cerro Buenavista, between Buvis summit and lower slopes of Frío, Buenavista massif, Weston 5845 (MO, NY). **San José/Cartago Border:** Cordillera de Talamanca, vicinity of Cerro Asunción, ca. 20.6 mi beyond El Empalme, Almeda & Wilbur 1605 (DUKE, F); Cordillera de Talamanca, ca. 7 km NW of Villa Mills in vicinity of Cerro de la Muerte, Almeda 2710 (CR, MO); ca. 35.4 km SSE of El Empalme off the Interamerican Highway, Cordillera de Talamanca, Almeda et al. 3381 (CAS, CR, F, GH, INB, K, MBM, MEXU, MO); ca. 28 km SSE of the La Cima turnoff from the Interamerican Hwy. on slopes of Cerro Sákira, Cordillera de Talamanca, Almeda & Wilbur 3426* (CAS, CR, INB, K, MO, MBM, NY); Cordillera de Talamanca ca. 35 km SE of El Empalme and ca. 11 km NE of Villa Mills, Almeda et al. 4251 (CAS); just below the highest point on the Interamerican Highway, NW of La Asunción, Burger & Baker 9518 (F, MO); near Asunción at the summit of the Interamerican Hwy., Burger & Gentry 8541 (F); Cerro Buena Vista, Cerro de la Muerte, Panamerican highway, Cordillera de Talamanca, Fosberg 27316 (NY); Cerro de la Muerte, Liesner & Heithaus 241 (MO); Asunción (summit of Cerro de la Muerte) 83 km from San José on the Pan American Highway, Mori & Anderson 207 (F); edge of the páramo ca. 2 mi NW from La Asunción on the Carretera Interamericana towards El Empalme, Wilbur & Almeda 17391 (DUKE, F); ca. 2 km SE of La Georgina and 8.3 km SE of La Asunción along the Carretera Interamericana, Wilbur 21192 (CAS, DUKE); slopes of Cerro Sákira at the Páramo Buenavista, Wilbur et al. 23754 (DUKE, F); on the upper slopes of Cerro Zacatales ca. 1 km NW of Asunción, the high point on the Interamerican Highway, Wilbur et al. 23994 (DUKE, F); in the vicinity of Páramo Jaboncillo ca. 84 km on the Carretera Interamericana, Wilbur 32416 (DUKE, MO). **Unknown location:** Páramo de Abejónal, Pittier 2278 (G); Páramo de Abejónal, Tonduz 7823 (BR[2], G); Cuesta de Tarrazu, Tonduz 7867 (P).

4. *Chaetolepis gentianoides* (Naudin) Jacq.-Fél., Bull. Mus. Nat. Hist. Nat., B, Adansonia, sér. 4, 16(2–4):272. 1995. (Figs. 6 g–i; 13). *Nerophila gentianoides* Naudin, Ann. Sci. Nat. Bot., sér. 3, 14:120. 1850. TYPE: SENEGAL: swamps along the rivers of Senegambia, Heudelot 668 (HOLOTYPE: P, internet image!; ISOTYPES: DS!, K!, P[2], internet images!).

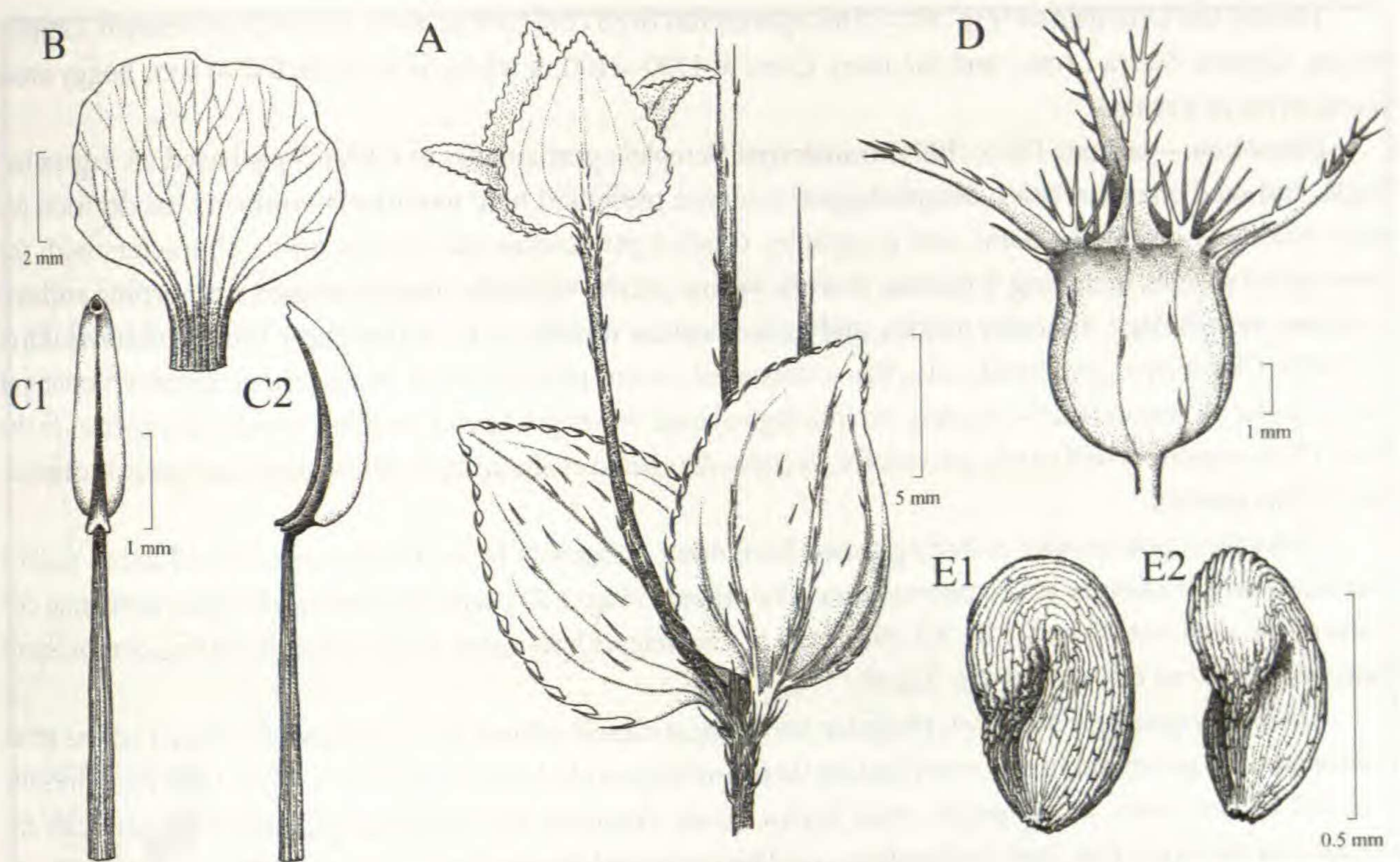


FIG. 13. *Chaetolepis gentianoides*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Jacques-Félix 235, P).

Erect, moderately to compactly branched, annual herb 10–40 cm tall. Distal cauline internodes quadrate and sparsely to moderately covered with appressed, smooth eglandular trichomes 1 mm long. Distal cauline nodes sparsely to moderately covered with appressed, smooth eglandular trichomes 1.5–2 mm long. Stems sparsely covered basally with antrorsely spreading, smooth, eglandular trichomes 1.5–2 mm long. Principal leaves membranaceous; adaxial surface spreading, smooth eglandular trichomes 0.5–1.0 mm long. Principal leaves membranaceous; adaxial surface sparsely to moderately covered with minute, smooth eglandular trichomes that are antrorsely spreading and evenly distributed over the entire surface; abaxial surface moderately strigose with minute smooth eglandular trichomes on the primary and secondary veins, sparsely covered with the same trichomes between the higher order veins; blades 5–20 × 4–7 mm, ovate to elliptic, apex acute, base ranging from acute to cuneate or rounded, (3)–5-nerved, with one (sometimes two) pairs of secondary veins arising at the base; margins ciliate-crenulate; inflorescence terminal, flowers typically solitary but sometimes paired or borne in a simple 3-flowered dichasium. Bracts similar to primary leaves. Bracteoles 3.5–11 × 1–1.5 mm, linear, oblanceolate to narrowly obovate, 3-nerved, basally to primary veins. Flowers subsessile or with pedicels 0.5–1.1 mm long, glabrous to minutely strigillose. Hypanthia (at anthesis) 2.5–4 × 2–3 mm, campanulate, sparsely to moderately covered with spreading, smooth eglandular trichomes 0.5–0.8 mm long; hypanthia (at maturity) with prominent vascular ribs when dry. Calyx lobes 1.5–2.6 × 0.8–1.2 mm, erect (sometimes spreading), narrowly triangular, apically acute; calyx lobes with smooth eglandular trichomes near the base; margins ciliate; intercalycine lobe sinus with a stalked, bifurcate or trifurcate trichome (stipitate-stellate, fide Wurdack, 1986). Petals 2–5 × 5–8 mm, yellow, apically obtuse and filaments 2–5 mm long, yellow; anthers 2–3 × 0.5 mm, yellow, tipped with a terminal trichome, glabrous, entire. Filaments 2–5 mm long, yellow; anthers 2–3 × 0.5 mm, yellow, low, linear or somewhat arcuate; pore dorsally inclined; connective prolonged 0.2–0.4 mm below the thecae. Ovary sparsely covered apically with smooth eglandular trichomes; style 4–6 mm long, yellow, glabrous. Seeds 0.4–0.6 mm long, light brown. Chromosome number: $n = 9$.

Flowering.—November through March.

Habitat and Distribution (Fig. 14).—This species has been collected in West Africa from Senegal, Guinea-Bissau, Guinea, Sierra Leone, and the Ivory Coast at 1700–2100 m where it is restricted to wet, boggy areas along rivers or streams.

Discussion.—Jacques-Félix (1995) transferred *Nerophila gentianoides* to *Chaetolepis* based on vegetative, floral, and seed characteristics. Morphological evidence presented here tentatively confirms his decision despite differences in seeds, habit, and geography. *Chaetolepis gentianoides* shares many characters with the neotropical species including 4-merous flowers, yellow petals, ventrally unappendaged isomorphic anthers, trichome morphology, 4-locular ovaries, and a chromosome number of $n = 9$ (Favarger 1962; Bolkhovskikh et al. 1969). *Chaetolepis gentianoides* also has a consistent nested position in all phylogenetic reconstructions of the genus in the second analysis using morphological data. It has not been possible to study this species in the field. DNA sequences will surely provide the decisive data set to evaluate the relationships and generic disposition of this species.

Chaetolepis gentianoides is distinguished from other congeners by its herbaceous annual habit, stalked and branching trichomes at the intercalycine lobe sinuses (Fig. 13D), and the convex elongate periclinal cell walls of the seed testa (Fig. 6 g–i). All other taxa of *Chaetolepis* have more or less interdigitating compressed/flattened periclinal cell walls (Figs. 5 & 6).

Among congeners, *Chaetolepis phelpsi* seems most closely related to *C. gentianoides* based on the strict consensus tree generated in this study and on their similar morphological characters. They both have dorsally inclined anther pores, yellow petals, ovate leaves, ciliate-crenulate leaf margins, and smooth eglandular trichomes on the hypanthia, both leaf surfaces, cauline nodes and internodes.

Chaetolepis phelpsi differs from *C. gentianoides* by its perennial woody habit, abaxial leaf surface that is punctate with eglandular and glandular trichomes, forked trichomes between the calyx lobes; and calyx lobes with sessile glands intermixed with eglandular and glandular trichomes.

Additional specimens examined: **GUINEA:** Dalaba, Chevalier 34349 (P); Timbo, Chevalier 18430 (G); Kindia, Farmar 214 (BM, K); Kindia, Jacques-Félix 235 (P); Benna, Jacques-Félix 7152 (P); Labe: Village of Vers Seriba, Jacques-Georges 8071 (MO); Labe, Roberty 6507 (G); location unknown, collector not given 16249 (K); Kala, collector not given 7376 (K). **GUINEA BISSAU:** Mangel near Dalaba, Adames 401 (K); Boe, Pereira 3017 (G); Boe, between Medina and Dandum, collector not given 2892 (K, P); Labe, collector not given 51519 (K); Faoual – Kakoni, collector not given 51248 (K). **IVORY COAST:** Sindou et al. 1131 (MO). **SIERRA LEONE:** Kabala, Mt. Loma, Jacques-Georges 176 (MO); summit of Bintimane Peak at 6390 ft, T.S. Jones 101 (K); Bintimane Peak, Jones 83 (K); Loma Mountains below Bintimane, J.K. Morton 392 (K); Bumban, Morton 2915 (K).

5. *Chaetolepis lindeniana* (Naudin) Triana, Trans. Linn. Soc. London 28:51. 1871. (Figs. 5 d–f; 15). *Haplodesmium lindenianum* Naudin, Ann. Sci. Nat. Bot., ser. 3, 14:150, pl. 5, fig 4. 1850. TYPE: VENEZUELA: in the Andes near Trujillo and Mérida, Linden 402 (HOLOTYPE: P!, photos: F!, GH!, NY!; ISOTYPES: BM!, BR![2], F!, G!, GH!, K![2], MA, internet image!, MPU, internet image!).

Trimeranthus alpestris Karsten, Linnaea 30:159. 1859. *Chaetolepis alpestris* (Karsten) Triana, Trans. Linn. Soc. London 28:51. 1871. Syn. nov. TYPE: VENEZUELA: in Boconó, Mérida, Karsten s.n. (HOLOTYPE: BM!; ISOTYPES: BR!; NY, internet image!).

Erect, much-branched shrub, 1–2.5 m tall. Distal cauline internodes quadrate, densely covered with trichomes 0.5–2 mm long that are tapered and sparsely roughened distally but thickened and greatly roughened at base (bulla-based). Distal cauline nodes with trichomes like those of the distal cauline internodes but broader basally and longer. Older branches woody, terete, exfoliating with age. Principal leaves coriaceous, densely covered with antrorsely spreading to appressed, bulla-based trichomes on the adaxial leaf surface; abaxial leaf surface densely covered with antrorsely spreading, barbellate trichomes on the primary and secondary veins like those of the distal cauline internodes; trichomes between the elevated primary and secondary veins like those on the primary and secondary veins but shorter; blades (3–)3.5–7(–9) × (1.5–)2.5–4.5 mm, ovate to elliptic-ovate, obtuse apically and basally (often broadly acute apically), 3-nerved; margins conspicuously revolute and fringed with bulla-based trichomes; petioles 1–1.5 × 0.5–0.7 mm, covered with trichomes like those of the nodes and internodes. Inflorescence terminal or axillary on lateral shoots, flowers solitary or in simple 3-flowered dichasia. Bracts identical to primary leaves. Bracteoles 3–5 × 2–3 mm, like the primary leaves but smaller. Floral pedicels 2–5 mm long, strigose like distal cauline internodes. Hypanthia (at anthesis) 2.5–3 × 2–2.5 mm,

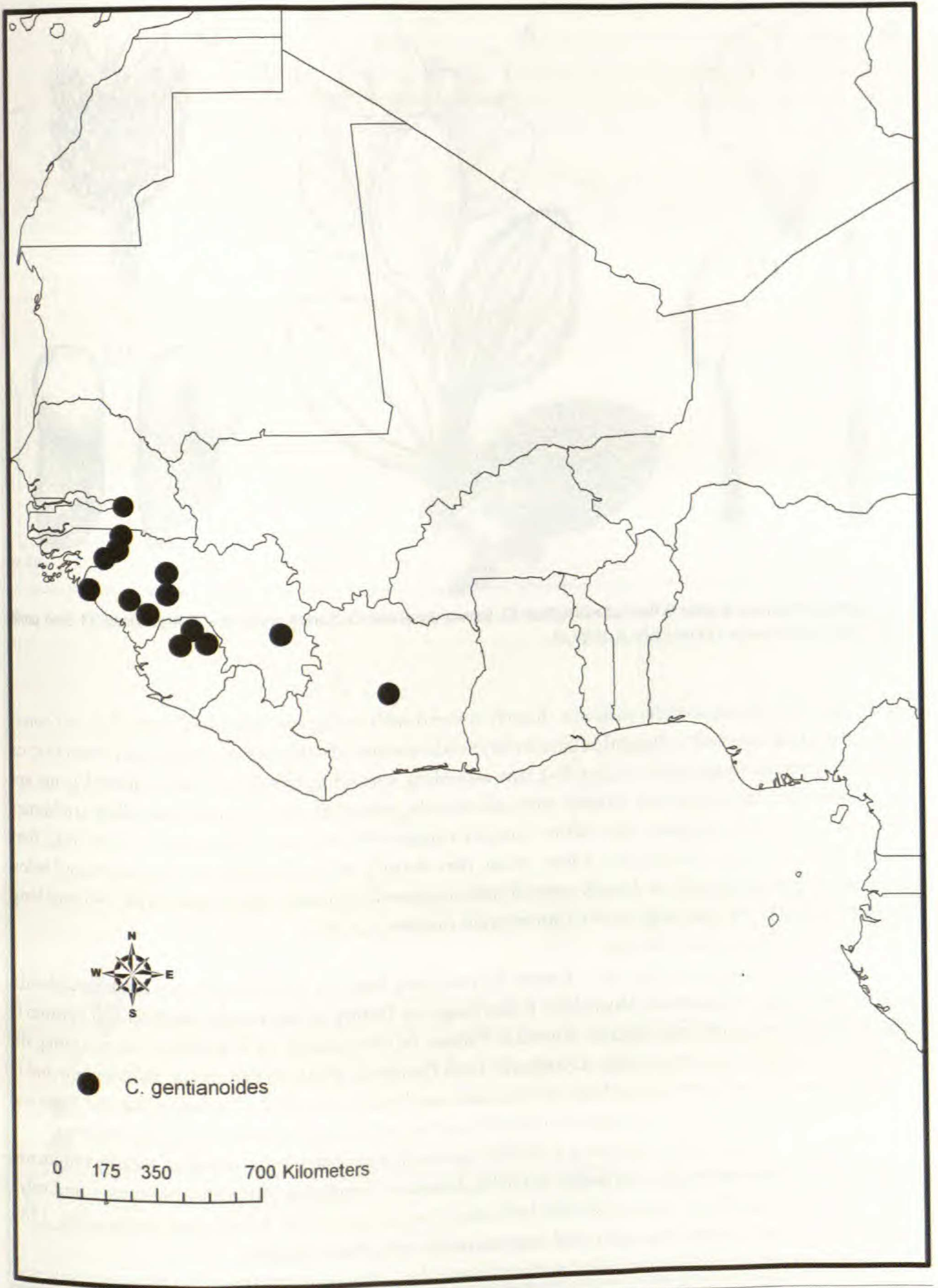


FIG. 14. Distribution of *Chaetolepis gentianoides*.

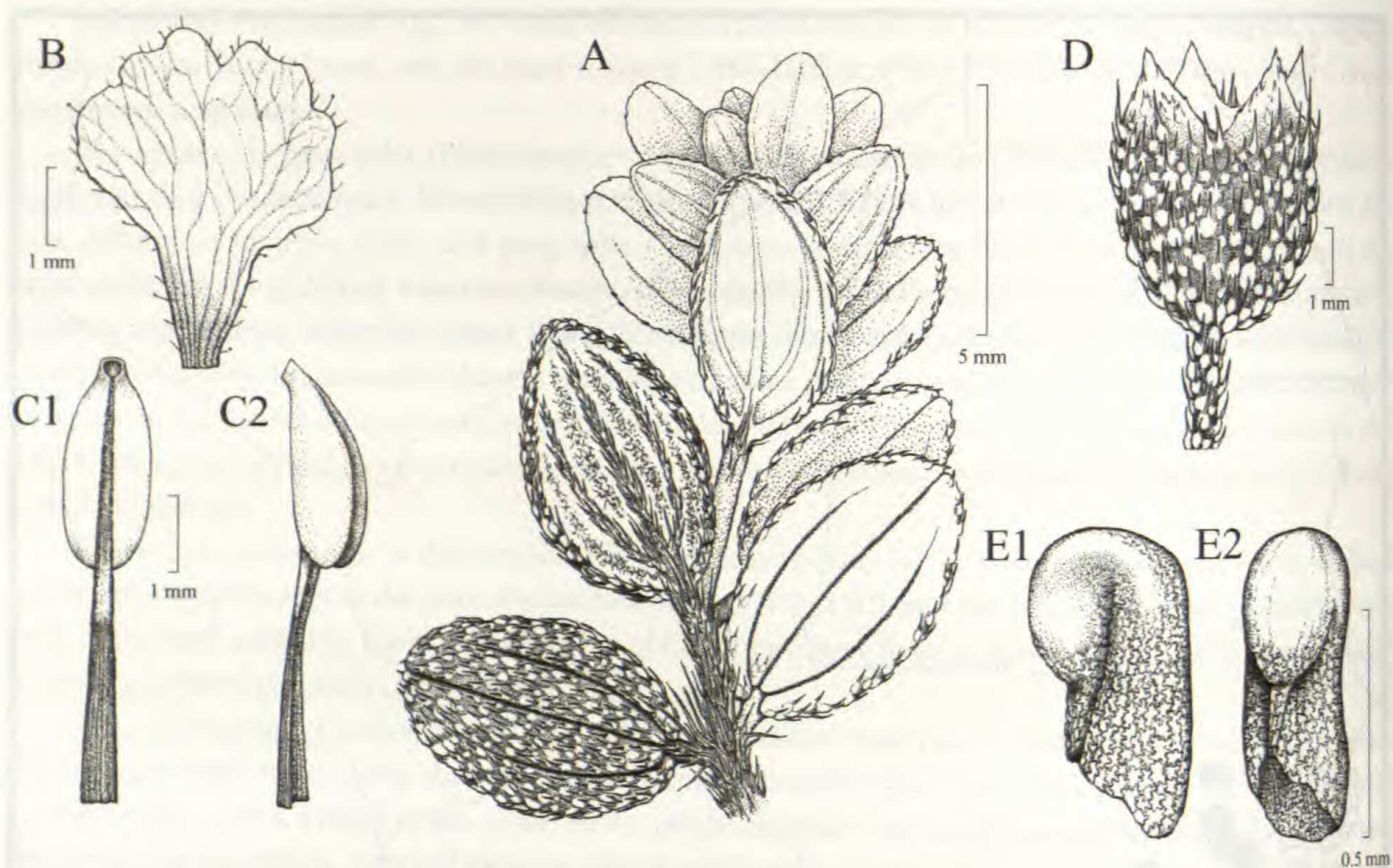


FIG. 15. *Chaetolepis lindeniana*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from King et al. 10481, F).

campanulate to subcampanulate, magenta, densely covered with antrorsely, appressed barbellate trichomes like distal cauline internodes, hypanthia (at maturity) with vascular ribs that are inconspicuous when dry; calyx lobes (on mature hypanthia) 1–1.5 × 0.8–1 mm, ascending, spreading, or reflexed, lance-deltoid, acute apically, ciliate; calyx lobes copiously strigose; intercalycine lobe sinus with one or several barbellate trichomes. Petals 5–6 × 2.5–4 mm, magenta, apex obtuse, margin fringed with trichomes. Filaments 3–4 mm long, dark magenta; anthers 1–1.5 × 0.4–0.6 mm, yellow, linear; pore dorsally inclined; connective not prolonged below the thecae. Ovary moderately to densely covered with roughened trichomes at the apex; style 7–8 mm long, magenta. Seeds 0.6–0.8 mm long, brown. Chromosome number: $n = 18$.

Flowering.—Throughout the year.

Habitat and Distribution (Fig. 16).—Known in Venezuela from the Cordillera de los Andes in Mérida, from Páramo Cupis to Páramo de Mucuchíes. It also ranges to Táchira in Páramo del Batallón and Páramo El Rosal. In Trujillo it occurs from Páramo Turmal to Páramo de Guaramacal. In Colombia it occurs along the Cordillera Oriental in the Department of Santander from Páramo de Berlín to Páramo de Mogotocoro and in several páramos in the Department of Norte de Santander north and east to Parque Nacional Natural Tamá and vicinity. Commonly collected along exposed roadsides and on rocky slopes in páramo at 2500–4000 m.

Discussion.—*Chaetolepis lindeniana* is a shrubby species distinguished by its elongate, basally roughened trichomes on cauline internodes and nodes, abaxial leaf surfaces, hypanthia, intercalycine sinuses, and calyx lobes. Other distinguishing features include bulla-based trichomes on the adaxial leaf surface (Fig. 15A), roughened trichomes on the ovary apex, and magenta petals with ciliate margins.

The closest relative of *Chaetolepis lindeniana* appears to be *C. santamartensis* based on the strict consensus tree generated in this study. Both species have roughened trichomes on the cauline internodes and nodes, abaxial leaf surfaces, hypanthium base, intercalycine sinuses, and calyx lobes. The two taxa also have entire ciliate leaf margins, magenta petals that are ciliate, and anthers with a dorsally inclined pore.

Chaetolepis santamartensis differs from *C. lindeniana* in having slightly roughened trichomes (vs. densely

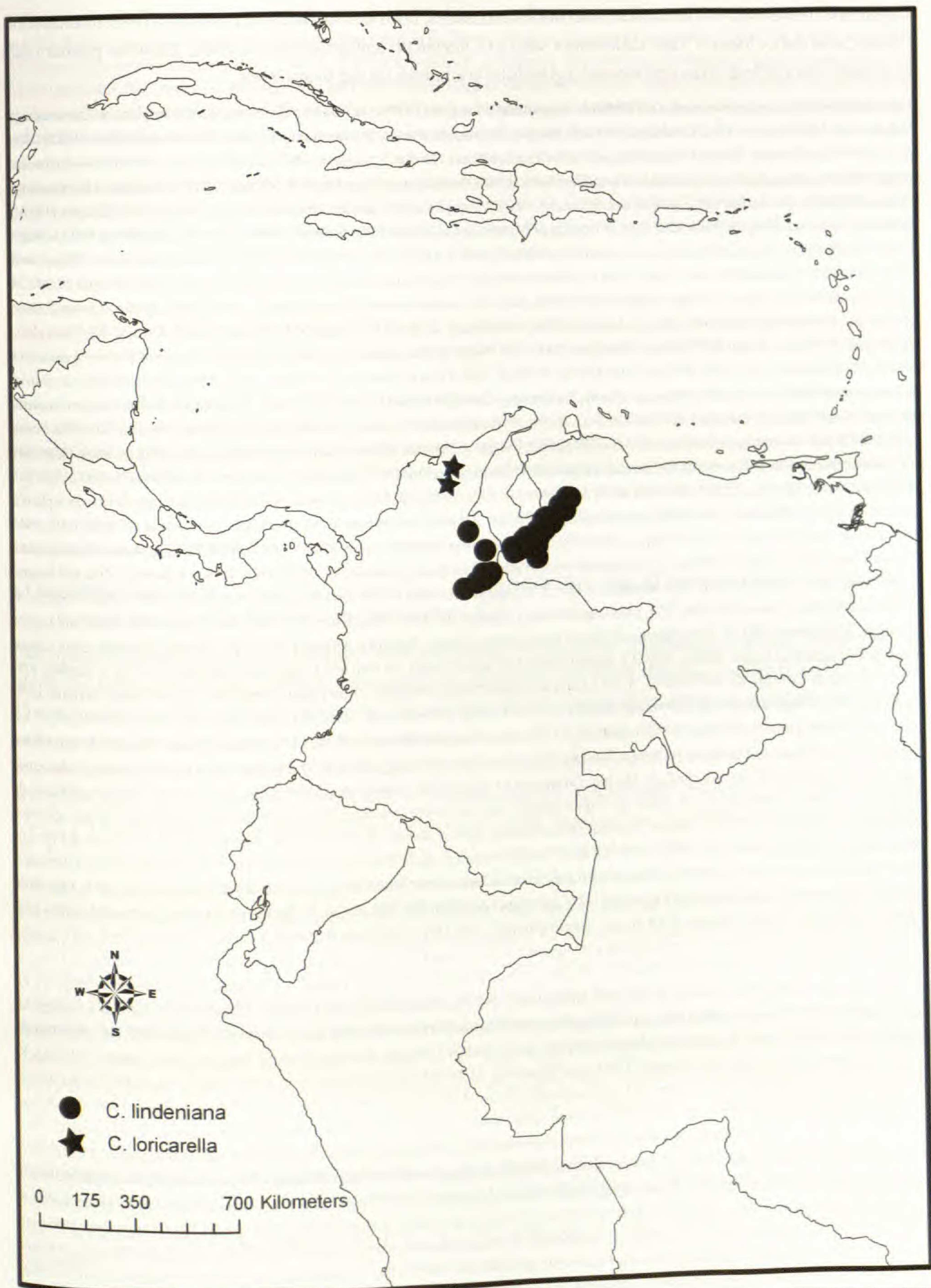


FIG. 16. Distributions of *Chaetolepis lindeniana* and *C. loricarella*.

roughened trichomes) on the cauline internodes and nodes, both leaf surfaces, hypanthium base, intercalycine sinuses, and calyx lobes. Other differences seen in *Chaetolepis santamartensis* include glabrous primary and secondary abaxial leaf veins and smooth eglandular trichomes on the ovary apex.

Representative specimens examined: **COLOMBIA. Santander:** 3 km from El Picacho toll booth on road from Pamplona to Bucaramanga, *Almeda et al.* 10630 (CAS, COL); Cordillera Oriental, Páramo de Santurbán, entre Bucaramanga y Berlín, *Barclay & Juajibioy* 10428 (COL, MO); Cordillera Oriental, Páramo de las Vegas, entre Berlín y Las Vegas, *Barclay & Juajibioy* 10452 (P); El Picacho, on road between Bucaramanga and Pamplona, *Barclay & Fernandez-Perez* 3726 (COL, FMB); Pamplona, La Baja, *Funck & Schlim* 1313 (P); Pamplona a Bucaramanga, Páramo de Berlín, *García-Barriga & Jaramillo* 20000 (CAS, GH, P); Pamplona por Garcia, *Garganta* 990 (US); Pamplona, *Kalbreyer* 1193 (K); Páramo de Romeral, *Killip & Smith* 8567 (GH, NY); edge of Páramo de Las Vegas, *Killip & Smith* 15698 (GH, NY); mountains E of Las Vegas, *Killip & Smith* 15801 (GH, NY); W slopes of Páramo Rico, *Killip & Smith* 17229 (F, GH, NY); Páramo de Mogotocoro, near Vetas, *Killip & Smith* 17651 (GH, NY); Páramo Rico, near Vetas, *Killip & Smith* 17666 (GH, NY); Páramo de las Puentes, above La Baja, *Killip & Smith* 18189 (GH, NY); de las Coloradas, above La Baja, *Killip & Smith* 18403 (GH, NY); Carretera entre Bucaramanga y Pamplona, *Murillo & Jaramillo Mejía* 1245 (COL, P); Municipio Charta, carretera hacia el Roble, *Orozco et al.* 1600 (COL); Pamplona, collector unknown s.n. (K); Entre el corregimiento de Vetas y el Alto del Picacho, *Villamizar* D14 (COL). **Norte de Santander:** Cordillera Oriental, Chorreon de Comageuta, entre Alto de Almorzadero y Quebrada de Presidente, *Barriga* 10034 (F, NY); Hoya de Musticua, vertiente este (de Pamplona a Mutiscua), *Barriga & Cuatrecasas* 10264 (F, NY); Municipio de Cácuta, La Laguna, *Contreras et al.* 43 (HECASA); entre Pamplona y Berlín, margen izquierda carretera, *Cuatrecasas & Rodriguez* 27912 (COL, F, G, K, NY, P); Pamplona, por Garcia (sur de la ciudad), *Fábrega* 990 (F); Cucutilla, Vereda Carrizal, Páramo El Romeral, *Galván et al.* SYG1025 (COL); E slope of Páramo de Santurbán, toward Mutiscua, *Killip & Smith* 19596 (GH, NY); Municipio de Cucutilla, vereda El Carrizal, Páramo de El Romeral en límites con Santander, *Sanchez et al.* 5088 (COL, HECASA); Herrán, Tamá, Sector Orocué, 7°25'31"N, 72°26'38"W, *Mendoza et al.* 7252 (FMB, HECASA); Municipio de Pamplona, Cerro del Río Pamplonita, *Sánchez & Solano* 4862 (HECASA); Municipio de Chitagá, Páramo del Almorzadero, sector de Presidente, *Sánchez et al.* 10383 (HECASA); Provincia de Pamplona, páramos de la baja, *Schlim* 1739 (BR). **Unknown location:** *Jeuxei* 850800 (BR). **VENEZUELA. Lara:** Municipio Moran, trail from Humo-carro to Buenas Aires (Caserío) below Páramo Los Rosas, *Liesner et al.* 8030 (MO); between Buenos Aires and Páramo de las Rosas, *Steyermark* 55483 (F, NY). **Mérida:** 6.4 km SE of Laguna Mucubají off the road to Barinas, *King et al.* 10481 (CAS, F); Sierra Nevada above Mérida, *Alston* 6843 (BM, NY); near Laguna Negra, Páramo de Mucuchies, *Alston* 6937 (BM, NY); Laguna Mucubají and Laguna La Negra, *Aristeguieta* 2453 (F, NY); Páramo de Mucuchies, distrito Rangel, *Aymard & Ortega* 1349 (CAS); distrito Miranda, entre Laguna Mucubají y Laguna La Negra, *Badillo* 5543 (F); slightly below La Laguna Negra, on trail to La Laguna de Mucubají, *Barclay & Juajibioy* 9799 (MO); Páramo de Conejos, *Bernardi* 680 (G, K, NY); Páramo Laguna Negra, Mucubají, entre Laguna Grande et Laguna Negra, *Bernardi* 10793 (G, K, MO, NY); Páramo de la Negra, *Bernardi* 10838 (F, G, K, NY); *Ibid.*, *Bernardi et al.* 16962 (K); Santo Domingo, *Bogner* 829 (K, M); 67 km NE of Mérida along road to Barinas, *Breteler* 3346 (G, NY, P); near Chachopo, *Bruijn* 1025 (MO, US); distrito Rangel, Páramo de Mucuchies, ascending from Hotel Los Frailes to the base of Picocha El Gavilon, *Carpenter & Joyal* 880 (NY); Piñango, hoyo del Río Chirurí, *Cuatrecasas et al.* 28042 (F, G, K, NY); Sierra Nevada de Mérida, Páramo en La Quebradita, *Cuatrecasas* 28104 (GH); entre Pueblo Nuevo y el Páramo de Quirorá, Las Tapias, *Cuatrecasas et al.* 28474 (F); Laguna Negra, Sierra de Santo Domingo, *Dennis* 2050 (K); distrito Rangel. Páramo de Santo Domingo, near Hotel Los Frailes, Parque Nacional Sierra Nevada, *Dorr & Barnett* 5182 (CAS, NY); distrito Rangel, la cuenca del Río Los Granates, west and east banks of the Río Los Granates, Parque Nacional Sierra Nevada, *Dorr & Barnett* 5577 (NY, P); distrito Libertador, Loma Redonda, Laguna Los Antojos, *Fernández* 441 (MO); Sierra Nevada de Santo Domingo, Loma del Baho alrededores de la Laguna de Valencia, cercanías de Santo Domingo, *Figueiras* 8733 (CAS); *Funck & Schlim* 864 (BM, BR [4], P); Páramo de Partahuelo, *Funck & Schlim* 1266 (BM, P); Carretera Andina, Páramo de La Negra, *García-Barriga* 13301 (NY); Quebrada de Saisay, *Gehriger* 37 (GH, F, MO, NY); Laguna Negra, *Gines* 1732 (NY); E of the moranine systems of Laguna Victoria, along Hwy. 7, *Hanselmann & Loveless* 27 (DUKE); Páramo de Conejos, *Hanbury-Tracy* 111 (NY); Laguna Negra, *Hueck* s.n. (F); Sierra Nevada de Santo Domingo, versant NW Laguna Negra, *Humbert* 26408 (NY, P); *Ibid.*, *Jacquemoud* 233022 (G); Páramo de San José, *Jeffrey et al.* 2142 (K); trail leading from El Royal, between Las Escaleras y La Negrita, *Luteyn* 6098 (CAS, NY); trail leading from La Negrita downstream towards Puente de La Escalera, *Luteyn* 6167 (CAS, MO, NY); Pico Espejo, *Mägdefrau* 650 (M); al norte de la carretera Mérida-Barinas, *Meier* 1132 (M); Páramo de Santo Domingo, Laguna Negra, *Moritz* 1591 (CAS, K, P); El Valle, *Oberwinkler* 13420 (M); Anden, El Rincon, *Oberwinkler* 12397 (M); Quebrada de Saisay, *Pittier* 37 (G); San Rafael de Mucuchies, along river, *Pittier* 12910 (G, NY); Páramo de Laguna Grande, *Pittier* 13245 (F, G, K, NY); below Cañada Cerrada, *Pittier* 13289 (F); distrito Rangel, Laguna Negra, *Quintero* 127 (MO); distrito Libertador, Sierra Nevada de Mérida, alrededores de la Laguna Verde, al pie del Pico Humboldt, *Ruiz-Terán* 2303 (DUKE); San Rafael, entre los caseríos de El Molino y El Portachuelo, Distrito Chacón, *Ruiz-Terán* 3061 (P); alrededores de Laguna Azul o del Corazón, Páramo de los Granates, Sierra Nevada de Santo Domingo, distrito Rangel, *Ruiz-Terán* 6356 (P); Páramo de Minugú, unos 10 km al SE de San Rafael de Mucuchies, *Ruiz-Terán* 7193 (BR, F); parte media del valle en U de La Mucuchache, al sur del Páramo de Apartaderos, Cordillera de los Andes, a orillas de la quebrada La Mucuchache, afluente del Río Chama, distrito Rangel, *Ruiz-Terán & López-Figueiras* 289 (F, P); orillas de la quebrada de Piedras Blancas, unos 2 km al norte del Pico de Piedras Blancas, en la ruta hacia el sitio Los Caracoles, Cordillera de los Andes, distrito Justo Briceño, *Ruiz-Terán & López-Figueiras* 348 (F, P); Páramo de San José abajo de la Piedra de Pirela, vertiente de Mucutuy, Cordillera de Los Andes, distrito Arzobispo Chacón, *Ruiz-Terán & López-Figueiras* 727 (F, P); El Alto, Páramo de El Jabón, abajo de los límites del estado Trujillo, Cordillera de los Andes, *Ruiz-Terán & López-Figueiras* 877 (P); Páramo de Mijará, Cordillera de los Andes, unos 15 km al NNE de la aldea Chacantá, municipio Libertad, distrito Arzobispo Chacón, *Ruiz-Terán & López-Figueiras* 1506 (F, US); Páramo de Quirorá (o de Chacantá), Cordillera de los Andes, municipio Estanques, distrito Sucre, *Ruiz-Terán & López-Figueiras* 1685 (MO); Páramo de Quirorá (o de Chacantá), Cordillera de los Andes, municipio Estanques, distrito Sucre, *Ruiz-Terán*

& Lopez-Figueiras 1717 (NY); distrito Rivas Dávila, Páramo de El Batallón, entre la torre de TV y Laguna Grande, Ruiz-Terán & López-Figueiras 8307 (DUKE); Filo de La Vagabunda, entre las poblaciones de El Morro y Aricagua, distrito Libertador, Ruiz-Terán & López-Figueiras 9371 (MO); entre El Baramito y Las Porqueras, 7–10 km, al NE de la población de El Morro, vertiente suroccidental de la Sierra Nevada de Mérida, distrito Libertador, Ruiz-Terán & López-Figueiras 9441 (MO); Sierra Nevada, Páramo de la Feirier, Schlim 1738 (BR); Teleferico trail, Pico Espejo, between 2nd and 3rd station, Smith 1196 (NY); Páramo de la Negra, Smith & Jorgensen 3536 (F); between Timotes and Paramito, Steyermark 55729 (F, NY); páramos between Chachopo and El Aguila, Steyermark & Rabe 97183 (NY); above Mérida by teleferica station Loma Redonda, Taylor 670 (K); en las cercanías de los arroyos y en las faldas abrigadas de Mucubaji, Tamayo 4353 (F); valley above La Hechicera Mérida, Tanner & Kapos 118 (MO); Páramo de Conejos, Tracy 111 (K); distrito Justo Briceño, near Almorzadero, along road, van der Werff & Ortega 6148 (CAS, MO); above the city of Mérida, slopes of Pico Espejo, Wolfe & Torres-Lesama 1296 (CAS); Páramo Cupis above San José, Distrito Arzobispo Chacón, Wurdack et al. 2769 (US); Páramo La Culata, N of the upper Río Mucujun, Zeeuw 9015 (NY); location unknown, Simmons 287 (K); San Rafael de Mucuchíes, along river, Zugegangen 12910 (M); below Cañada Cerrada, on wall along river, Zugegangen 13289 (M); Ibid., Zugegangen 469 (M). **Táchira:** Páramo Zumbador, Charpin & Jacquemoud 13384 (F, G, K); Páramo del Batallón, Quebrada Ferruginosa, Cuatrecasas et al. 28404 (F); trail leading to summit of Páramo de Tamá, Luteyn et al. 5320 (CAS, NY); NNE slopes of Pata de Judío, Luteyn et al. 5943 (CAS, F, NY); Páramo de Portachuelo, Luteyn et al. 6021 (CAS, NY); distrito Uribante, 19–21 km SE of La Grita on road to San José de Bolívar, Páramo del Batallón-Páramo El Rosal area, Luteyn & Lebron-Luteyn 9884 (CAS, MO, NY); laderas pantanosas al pie de peñascos de arenisca de Pata de Judío, entre Alto de Cruces y el páramo arriba de la Quebrada Teleférica, cerca de la frontera Colombia-Venezuela, Steyermark & Dunsterville 101162 (G, NY); Páramo de Tamá, en la region calcárea, cerca de la frontera Colombia-Venezolana, Steyermark & Dunsterville 98736 (M). **Trujillo:** La Morita, arriba de Jajó, Aristeguieta & Medina 3467 (NY); distrito Boconó, Páramo de Guaramacal, 20 km al E de Boconó, Aymard et al. 2922 (NY); NW slopes of La Reinosá, above La Mesa de Esnujaque, Box & Alayon 3810 (BM); distrito Urdaneta, Páramo La Providencia, Colella et al. 1212 (NY); distrito Carache, Páramo Turmal, SE of Pico Jabon, Dorr et al. 5306 (CAS, NY); El Atajo, cabecera de la quebrada El Riecito, vertiente suroccidental del gran Páramo de La Cristalina, distrito Trujillo, Ruiz-Terán 9002 (MO); entre Santa Rosalía y Cerro El Diablo, 0.5 km al este de Boconó, Solé 20 (NY); cumbre del Páramo de Guaramacal, entre Boconó y Guaramacal, Steyermark 104855 (NY).

6. *Chaetolepis loricarella* Triana, Trans Linn. Soc. London 28:51.1871 (Fig. 17). TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, Purdie s.n. (HOLOTYPE: BM?; ISOTYPE, K! [2]).

Erect, much-branched shrub to 1.2 m tall. Older internodes woody, terete, exfoliating with age. Distal cauline internodes terete and densely covered with appressed, narrowly lanceolate, flattened scales $0.5\text{--}0.75 \times 0.25\text{--}0.5$ mm that are basally attached with a raised thickening near the point of attachment, margins erose. Distal cauline nodes like internodes except scales slightly longer (0.75–1 mm). Principal leaves coriaceous, appressed-imbricate; adaxial surface glabrous apically, with a dense covering of minute appressed scales at the base of the blade; abaxial surface covered with two kinds of scales: apical region with narrow, elongate scales $1.5\text{--}2.5 \times 0.5$ mm adnate to the epidermis for their entire length, basal region beset with flattened erose scales like those of the upper cauline internodes; blades $3\text{--}5 \times 1\text{--}2$ mm, ovate to lanceolate, concave, tightly appressed with the abaxial side of the leaf facing outward and adaxial side facing inward toward the stem axis, apically acute, basally obtuse, with a single depressed vein visible only on the adaxial side; margins seemingly entire but minutely and obscurely erose and/or fringed with sessile or subsessile flattened scales with irregularly erose margins; sessile or with petioles 0.25–0.5 mm long, covered with flattened erose scales abaxially. Flowers terminal, solitary and sessile. Floral bracts like the principal leaves in shape and size, subsessile or sessile. Hypanthia (at anthesis) $2.5\text{--}3.5 \times 1\text{--}2$ mm, broadly cylindrical to campanulate, densely covered with appressed scales like those of the distal internodes; hypanthia (at maturity) with ribs not evident when dry. Calyx lobes $1\text{--}1.5 \times 0.3\text{--}0.5$ mm, narrowly triangular, apically acute, margins ciliate, scales present at the base of the calyx lobes, glabrous toward the apex, persistent. Intercalyne lobe sinus usually with a single large scale. Petals $7\text{--}10 \times 3\text{--}7$ mm, magenta, apically obtuse, margins ciliate. Filaments 5–6 mm long, magenta; anthers yellow, linear-oblong, bilobed ventro-basally and with a single deflexed lobe $1\text{--}2 \times 0.25\text{--}0.5$ mm dorso-basally; connective prolonged 0.2–0.4 mm below the thecae; pore dorsally inclined. Ovary apex densely covered with scales. Style 8–11 mm long, magenta. Seeds 0.7–0.9 mm long, tan or light brown. Chromosome number: unknown.

Flowering.—May through July.

Habitat and Distribution (Fig. 16).—*Chaetolepis loricarella* is endemic to the Sierra Nevada de Santa Marta, Colombia at 2900–3700 m. Labels on available collections indicate that it occurs in grassy páramos and along stream beds.

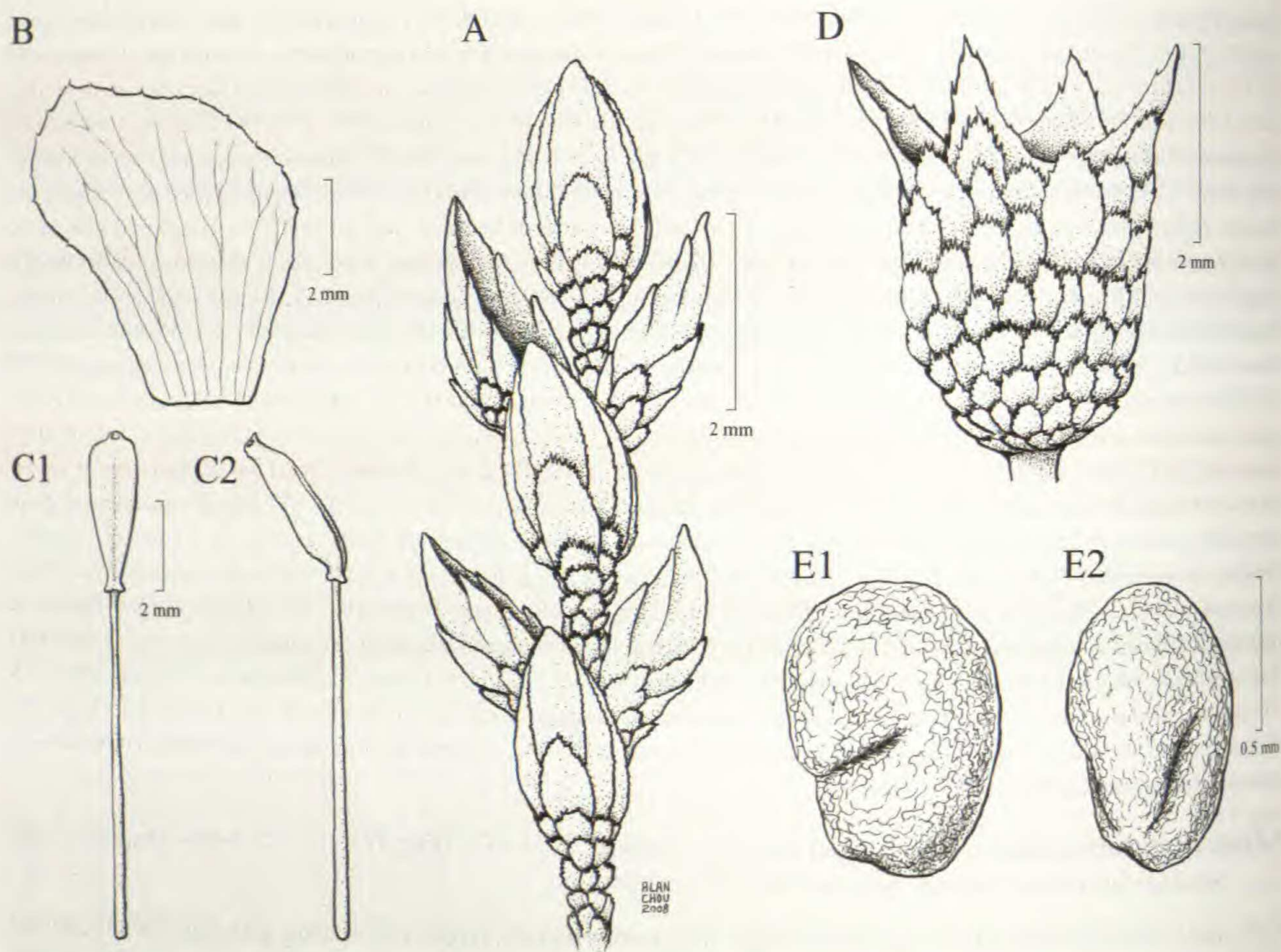


FIG. 17. *Chaetolepis loricaella*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Kernan 154, NY).

Discussion.—*Chaetolepis loricaella* does not appear to have any close relatives. It has unusual trichomes that are modified into flattened scales (Fig. 17A, D). These are found on the cauline internodes and nodes, both leaf surfaces, and hypanthia. In addition, this species has roughened trichomes on the ovary apex, a single primary vein on the leaf blade, and concave, appressed, imbricate coriaceous leaves with the abaxial surface facing outward and exposed and the adaxial surface facing inward toward the stem and concealed.

Representative specimens examined: **COLOMBIA.** César: Valledupar, Carbonó 3646 (COL, UTM); Mpio. Pueblo Bello, Village Nabusimake, first big ridge above the valley between Nabusimake and Pantano, in direction of Duitama, Stancik 893 (COL). Magdalena: Sierra Nevada de Santa Marta, Funck 393 (BR, P); Andredua, headwaters of Río Aracataca, Kernan 154 (COL, NY, US); N slope of Cuchilla Cinturagaca, next valley up from that of the Río Duriameina, White & Alverson 638 (COL, MO).

7. *Chaetolepis microphylla* (Bonpl.) Miq., Comm. Phyt. 72. 1840. (Figs. 5 g–i; 19). *Rhexia microphylla* Bonpl., Rhex. 4, pl. 2. 1806–1808. *Osbeckia microphylla* (Bonpl.) DC, Prodr. 3:140. 1828. TYPE: COLOMBIA or VENEZUELA: Bonpland s.n. (HOLOTYPE: P!; ISOTYPE: COL, internet image!).

Erect, compactly branched subshrub 10–50 cm tall. Distal cauline internodes quadrate, densely covered with elongate, moderately barbellate trichomes 0.5–1 mm long and smooth eglandular trichomes 1–2 mm long. Older branches woody, terete, glabrous or sparsely covered with moderately barbellate trichomes. Principal leaves coriaceous, somewhat unequal in each pair; adaxial leaf surface moderately covered with antrorsely spreading to appressed, moderately barbellate trichomes 0.1–0.5 mm long; abaxial leaf surface densely covered on and between primary and secondary veins with spreading or antrorsely spreading barbellate and dendritic trichomes 0.1–0.5 mm long with short or well-developed axes and a moderate number of spreading terete arms; blades 2–6 × 2–4 mm, ovate, rhombic, or rhombic-orbicular, acute (sometimes rounded or obtuse)

apically, cuneate to attenuate basally, adaxial surface with three nerves that extend for the entire length of the blade, sometimes 5-nerved with the outer pair arising from the base of the blade and extending one third to one half the length of the blade before converging with the margin; margins entire, sometimes revolute, ciliate; petioles 1–1.5 × 0.5 mm, glabrous. Inflorescence terminal, flowers solitary or borne in a simple 3-flowered dichasium. Bracteoles 2.5–5 × 2–3.5 mm, ovate, rhombic, elliptic, or obovate, indument of the adaxial surfaces like that of the principal leaves except for a glabrous basal region, indument of the abaxial surface identical to principal leaves, 3-nerved, petioles 0.5–1 mm long. Floral pedicels 0.5–1 mm long, moderately to densely covered with antrorsely spreading, moderately barbellate trichomes. Hypanthia (at anthesis) 2–3 × 2–3 mm, suburceolate to cylindrical, glabrous or sometimes sparsely beset distally with moderately barbellate trichomes on the vascular ribs; hypanthia (at maturity) with vascular ribs somewhat conspicuous on drying. Calyx lobes 1.5–2 × 1–1.5 mm, erect or ascending, lance-deltoid, apically acute, ciliate, beset with moderately roughened trichomes adjacent to the midrib but not along the margins; intercalycine lobe sinus with 1–3 smooth eglandular trichomes. Petals 2.5 × 2 mm, yellow, entire, apically obtuse with a single terminal barbellate trichome, margins glabrous. Filaments 2.5–3.5 mm long, pale brown when dry; anthers 0.2 × 0.4–0.6 mm, yellow, linear; pore ventrally inclined; connective prolonged 0.2–0.3 mm below the thecae. Ovary apex moderately to densely covered with smooth eglandular trichomes; style 0.5–0.6 mm long. Seeds 0.4–0.6 mm long, brown. Chromosome number: $n = 9$.

Flowering.—Throughout the year.

Habitat and Distribution (Fig. 19).—In Colombia this species is largely centered in the Cordillera Oriental (Boyacá, Cundinamarca, Norte de Santander, and Santander) with outliers in the Cordillera Central (Antioquia) and Cordillera Occidental (Cauca). In Venezuela it ranges from the state of Mérida west to Táchira. It occurs between 2000–3700 m.

Discussion.—*Chaetolepis microphylla* is readily recognized by its small leaf blades and its elongate moderately roughened trichomes on the cauline internodes, nodes, both foliar surfaces, and midrib of the calyx lobes.

Chaetolepis microphylla is most similar to *Chaetolepis santamartensis* based on morphological similarities and their positions on the consensus trees (Fig. 2). These species share entire, ciliate leaf margins, and roughened trichomes on the cauline internodes and nodes, both foliar surfaces, and midrib of the calyx lobes (Fig. 18).

Chaetolepis santamartensis differs from *C. microphylla* in having slightly roughened trichomes on the cauline internodes and nodes, both foliar surfaces, hypanthium base, intercalycine sinuses and calyx lobes, five (vs. three) elevated veins on the abaxial leaf surface; magenta, ciliate petals (vs. yellow and eciliate); and a dorsally inclined (vs. ventrally) anther pore.

Representative specimens examined: **COLOMBIA. Antioquia:** Municipio de Yarumal, Llanos de Cuivá, Acevedo et al. 1400 (COL); Municipio de Yarumal, Llanos de Cuivá, sobre la carretera al cementerio, Callejas et al. 2560 (NY); San Pedro, Daniel 1341 (F); Municipio de Santa Rosa, Lozano et al. 5988 (COL); Municipio de Entrerriós, ca. 3 km from Entrerriós on the road to Santa Rosa de Osos, downstream from bridge along banks of Río Grande, MacDougal & Roldan 3640 (CAS); highland of Santa Rosa, unknown collector 7542 (F, GH); en una meseta a 1 km al norte de Santa Rosa de Osos, Valderrama et al. s.n. (NY); Municipio San Pedro, km 4 of road San Pedro-Entrerriós, along roadside, Zarucchi 5865 (COL, MO); Highlands of Santa Rosa, collector unknown 7549 (K). **Boyacá:** Arcabuco, via Arcabuco-Villa de Leyva, Alonso JLF14181 (COL); Raquira, Castroviejo 10585 (MO); Carretera Raquira Cleef et al. 3459 (COL); Páramo de La Rusia, NW-N de Duitama, Cleef 7040 (COL); Municipio de Ramiriquí, Fagua 399 (COL); Desierto de La Candelaria, cerros alrededor del Convento, García-Barriga 20247 (COL, F, GH); Laguna Seca, beyond Alto del Oso, Grubb et al. 580 (COL, K); 2 or 3 km al nordeste de Villa de Leyva, Melampy 23 (FMB); Villa de Leyva. Subiendo por la montaña arriba del Hotel Duruelo, Mendoza 1153 (FMB); Paipa, Piscinas Municipales de Aguas Termales, Lomita arriba de piscinas, Silverstone-Sopkin 5423 (NY); Municipio Samaca, Vereda Ruchal-parte alta, Stancik 1308 (FMB); Cómbita, vereda de Santa Bárbara, Uribe-Uribe 6609 (NY); between Ubaté and Cucunubá, 5°16'8.9"N, 73°47'52.33"W, Wood 3699 (FMB). **Boyacá/Santander border:** 1 km beyond La Palma on road between La Palma and Gámbita, Almeda et al. 10496 (CAS, COL). **Cauca:** Cerro California, Cordillera Occidental, Becking & Negret BN271 (COL). **Cundinamarca:** Boqueron de Bogotá, Andre 736 (NY); Ibid., Arbeláez 605 (CAS); Zipaquirá, Arbeláez & Castañeda 1331 (NY); Bogotá, Ariste-Joseph s.n. (GH, NY, US); Páramo de Guasca, Balls 5686 (BM, K); Bogotá, quebrada Chicó, Black 46-405 (F); Cerro de Guadalupe, Barclay 4089 (COL); Macizo de Bogotá, quebrada de Chicó, Cuatrecasas 5009 (NY); Cerros de Bogotá, Daniel 1452 (F); Cerro de Monserrate, Duque-Jaramillo 2870 (COL, NY); Páramo de la Calera, Fernandez 2418 (BM); mouth of San Francisco Canyon, lower slopes of Cerro de Guadalupe, Bogotá, Fosberg 22166 (NY); Ibid., Funck & Schlim 1259 (P); Cordillera Oriental, Macizo de Bogotá, Guadalupe, García 113 (NY); Municipio Guasca, Páramo de Guasca, García-Barriga 6223 (COL, NY); Bogotá, Goudot s.n. (P); Road Sopó-Guasca, 6 km SE of Sopó, Grabandt & Huertas 20 (US); Guasca, Grant 7368 (GH); Bogotá, Hartweg 1000 (BM, BR [2]); Monserrate, Bogotá,

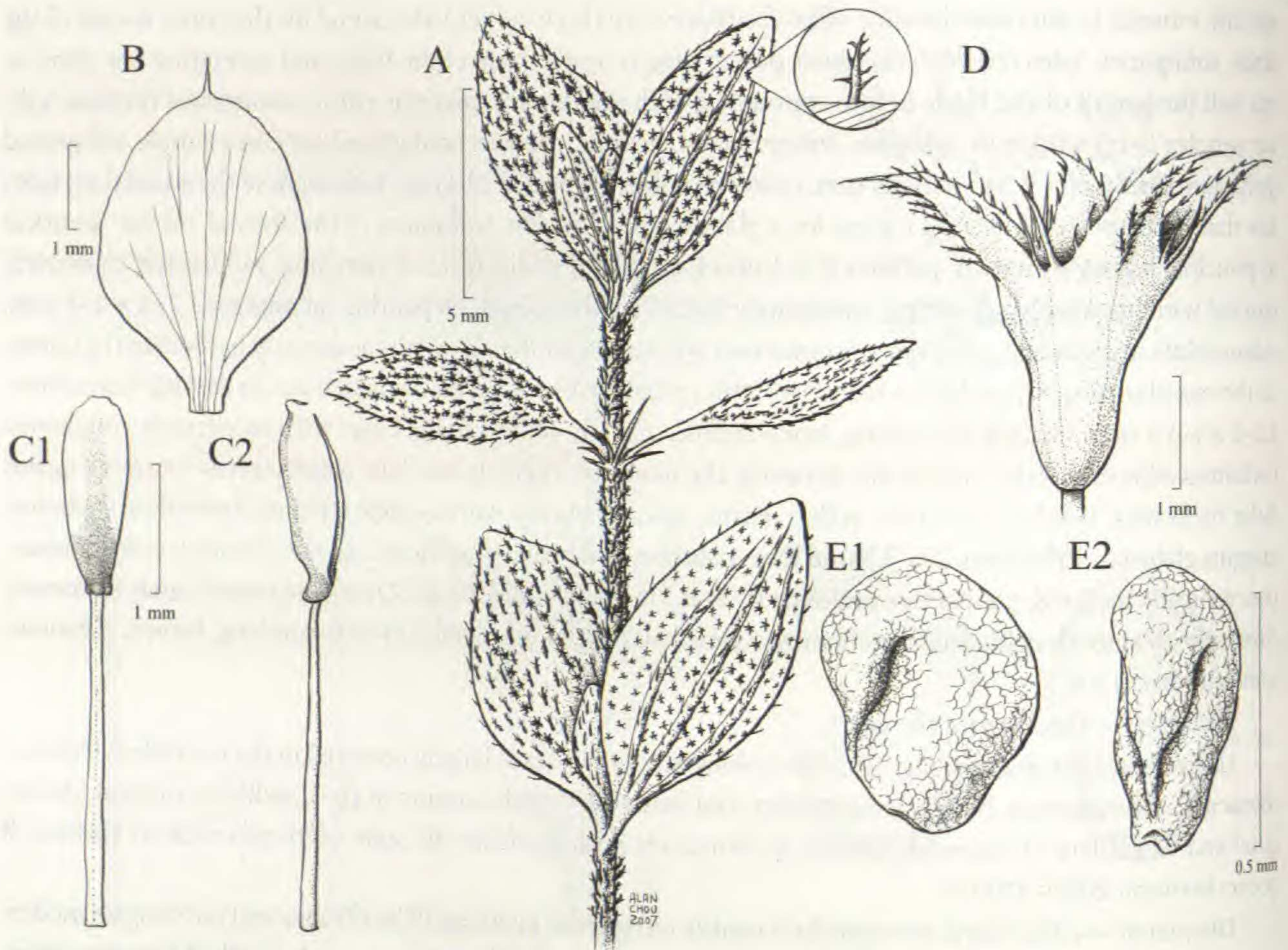


FIG. 18. *Chaetolepis microphylla*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Daniel 1341, F),

Haught 4986 (K, NY); Guadalupe, Bogotá, Haught 5654 (US); Vitelme, Hermann 11350 (NY); Bogotá, Holton 26 (NY); Bogotá, Holton 920 (GH); Municipio de Fómeque, Páramo de Chingaza, Huertas & Camargo 6489 (COL); montes, el Retiro-Chicó, cerca de Bogotá, Jaramillo 3478 (NY); Bogotá, Kalbreyer 818 (K); Bogotá, lomas sobre la calle 53, Lozano s.n. (COL); Linden 694 (BM, K, NY, P); Andes de Bogotá, Meayor 74 (BR); above Bogotá, Rusby & Pennell 1285 (GH, MO, NY); Julia Hill, Sabana de Bogotá, Schiefer 576 (CAS, GH); Macizo de Bogotá, Cerro El Retiro, Schultes 7075 (F, K); Macizo de Bogotá, quebrada Chicó near the city of Bogotá, Schultes & Villarreal 7089 (NY); mountains above Bogotá, Sprague 213 (K); Bogotá, Triana s.n. (BR, NY); Bogotá, unknown collector 057 (MO); Tocancipá, montes altos al oriente, Uribe-Uribe 5999 (COL, MO, NY); hills near Bogotá, Wier 192 (K); Bogotá, Wier s. n. (BR); Ubaté, Wood 3699 (K); location unknown, Wood 3510 (FMB, K); Bogotá, páramos in via ad Calera, Woronow & Juzepczuk 5106 (NY). **Norte de Santander:** Municipio de Cámeta, La Laguna, Contreras et al. 79 (HECASA); vertiente oriental, Pamplona, cerro al NE, Cuatrecasas & Garcia-Barriga 10209 (COL); Alrededores de Pamplona, Fabrega 666 (F); Pamplona, alto de las Coronadas, al sur de la ciudad, Fabrega 1293 (F); Sierra, Humbert 26732 (P); Municipio de Mutiscua, Vereda San José del Pino, Sánchez & Vargas 10580 (HECASA). **Santander:** Proyecto Parque Nacional Natural Yariguíes, San Vicente de Chucurí, Ardila et al. 121 (FMB); Páramo del Almorzadero, region media, Cuatrecasas 9944 (F); Pamplona a Sabaneta, camino de Cucutilla, Fabrega 752 (F); vicinity of California, Killip & Smith 16769 (GH, NY); vicinity of La Baja, Killip & Smith 17118 (F, GH, MO, NY); municipio de Onzaga, Vereda Chaguacá, Orozco et al. 1912 (NY). **VENEZUELA. Mérida:** Páramo de San José abajo de la Piedra de Pirela, vertiente de Mucutuy, Cordillera de los Andes, distrito Arzobispo Chacón, Ruiz-Terán & López-Figueiras 720 (F); Carretera Estanques-El Molino, 55 km de Estanques, Michel-angeli et al. 1268 (CAS, NY); Municipio de Onzaga, Vereda Chaguacá, Torres et al. 486 (COL); distrito Arzobispo Chacón, in páramo between San José and Mucutuy, Wurdack et al. 2773 (F, MO, NY, P, US). **Táchira:** Páramo-Zumbador, 14 km S of El Cobre, Gentry 11081 (MO); Los Mirtos, entre El Cobre y El Zumbador, al Borde de la Carretera, distrito Jáuregui, Ruiz-Terán et al. 8105 (F); subpáramo, 2 kms de Zumbador, entre Zumbador y Queniquea, Steyermark 105092 (DUKE, P); entre Boca de Monte y Zumbador, Steyermark & Rabe 96837 (NY); 2 kms de Zumbador, entre Zumbador y Queniquea, Steyermark 105092 (F, NY). **Unknown location:** Linden s.n. (BR).

8. *Chaetolepis perijensis* Wurdack var. *perijensis*, Phytologia 8:166. 1962. (Figs. 20 A–D1, E1, E2). TYPE: COLOMBIA. MAGDALENA: collected in páramo between Cerro Venado and Cerro Avion, Sierra de Perijá, 3270–3350 m, 8 Nov 1959. J. Cuatrecasas & R.R. Castaneda, 25118 (HOLOTYPE: US, internet image!; ISOTYPE: COL, internet image!).

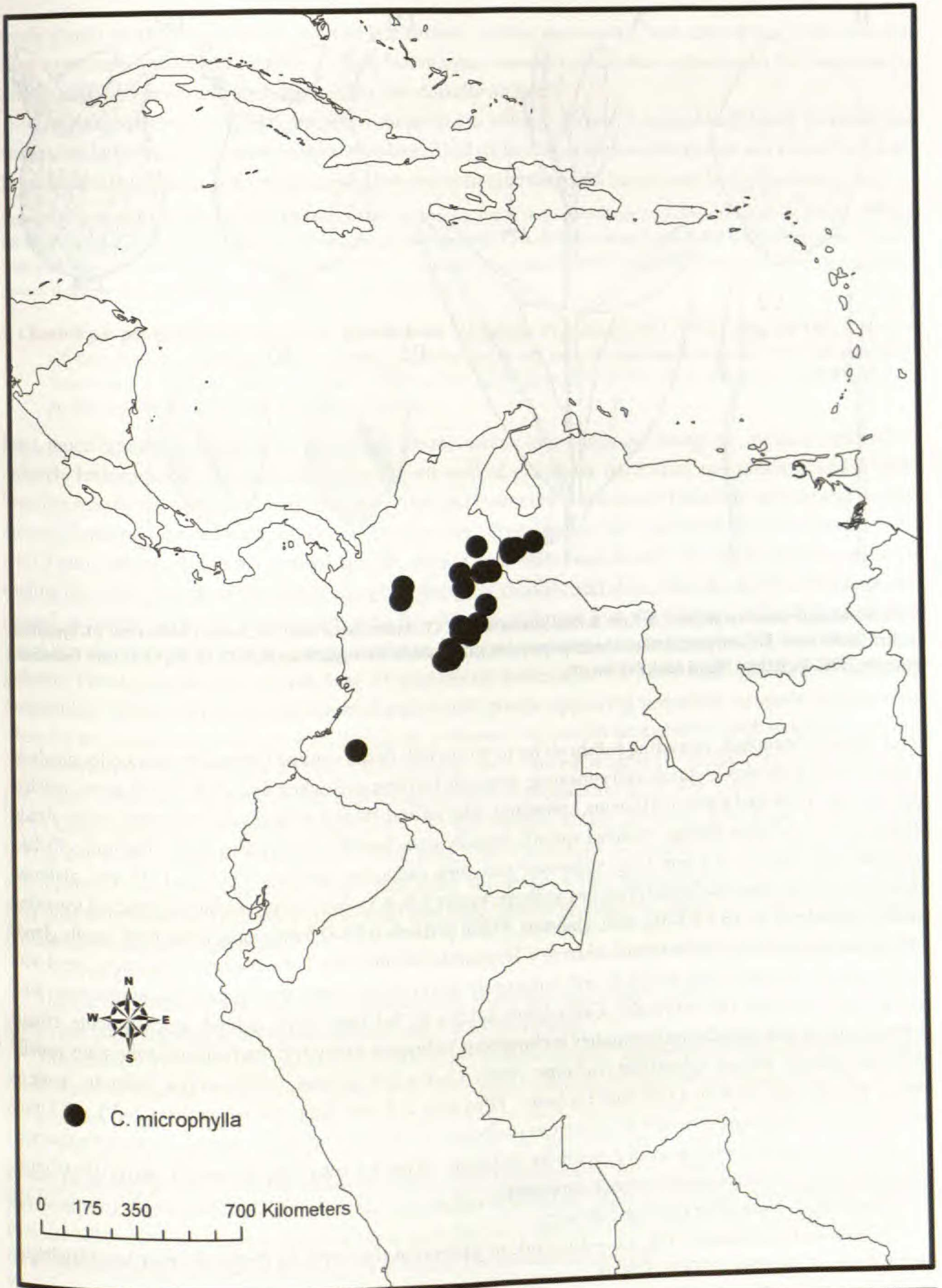


FIG. 19. Distribution of *Chaetolepis microphylla*.

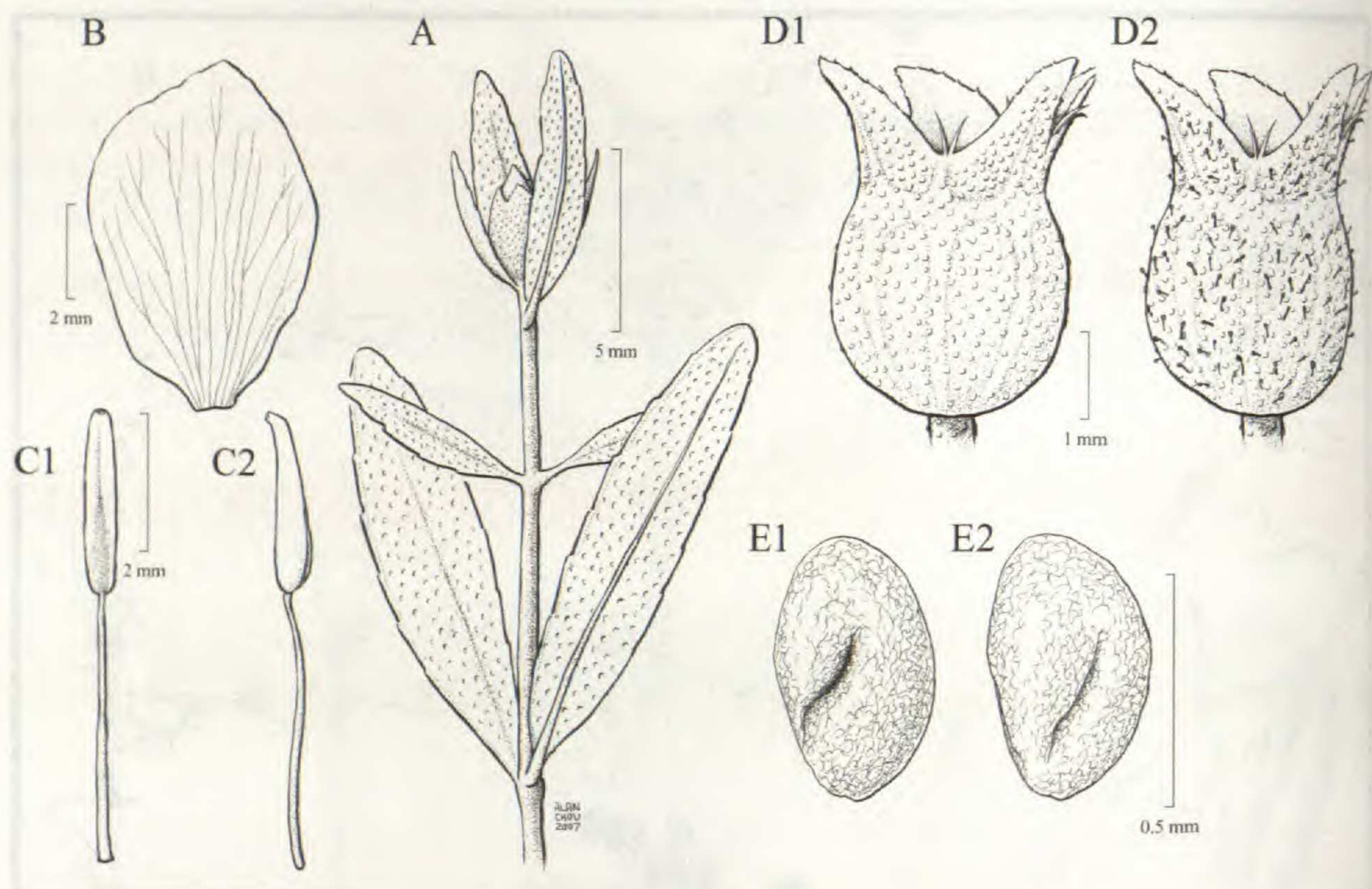


FIG. 20. *Chaetolepis perijensis* var. *perijensis*. A. Habit. B. Petal (adaxial surface). C1. Stamen (dorsal view). C2. Stamen (profile view). D1. Hypanthium. E1. Seed (profile view). E2. Seed (ventral view). *Chaetolepis perijensis* var. *glandulosa*. D2. Hypanthium (A, B, C1, C2, D1, E1, E2 from, Cuatrecasas & Castaneda, 25082, US; D2 from Tillett & Hönig 747-946, US).

Erect, densely branched, spreading subshrub up to 40 cm tall. Distal cauline internodes and nodes quadrate, winged, beset with sessile glands and appearing minutely furfuraceous when dry. Older stems terete, exfoliating with age. Principal leaves coriaceous, spreading, adaxial and abaxial surfaces covered with sessile glands; blades $5-8 \times 1-1.5$ mm, oblong, rounded apically, broadly acute basally, 1-nerved; margins obscurely ciliolate-serrulate, the cilia 0.1–0.2 mm long, appressed and often caducous; petioles $0.5-1.5 \times 0.25$ mm, glabrous. Flowers terminal, often on lateral branches, solitary; bracts $3.5-4.5 \times 0.5-1$ mm, similar to principal leaves but smaller; petioles $0.3-0.8 \times 0.1-0.2$ mm, glabrous. Floral pedicels 0.25–0.5 mm long, beset with sessile glands and appearing minutely furfuraceous when dry. Hypanthia (at anthesis) $3-4 \times 3-4$ mm, urceolate, beset with sessile glands and appearing minutely and caducously furfuraceous when dry; hypanthia (at maturity) with conspicuous vascular ribs when dry. Calyx lobes $1-1.5 \times 0.75-1$ mm, erect, deltoid, apically acute, ciliate, covered with sessile glands and a minutely furfuraceous indument when dry; intercalycine lobe sinus usually with one smooth, minute eglandular trichome. Petals $4.5-6 \times 2.5-3.5$ mm, yellow, entire, glabrous, acute to obtuse apically and lacking a terminal trichome. Filaments 2–3 mm long, yellow; anthers $2-2.5 \times 0.5$ mm, yellow, linear; pore dorsally inclined; connective prolonged 0.1–0.2 mm below the thecae. Ovary apex sparsely to moderately covered with smooth eglandular trichomes. Style 5–7 mm long, brownish. Seeds 0.4–0.5 mm long, pale brown. Chromosome number: unknown.

Flowering.—November through February.

Habitat and Distribution (Fig. 21).—Endemic to páramo in the Sierra de Perijá of César and Magdalena departments, Colombia at 3000–3350 m.

Discussion.—*Chaetolepis perijensis* var. *perijensis* is distinguished by its furfuraceous cauline internodes and nodes that are both furfuraceous and with sessile glands. The leaf blades are oblong with one primary vein, abaxially punctate, and entire.

The closest relative of *Chaetolepis perijensis* var. *perijensis* appears to be *C. alpina*. These taxa both have

sessile glands on the hypanthium, adaxial leaf surface, cauline internodes, and calyx lobes. Both taxa also share a punctate abaxial leaf surface, a ciliate leaf margin, smooth eglandular trichomes on the intercalycine sinuses and ovary apex, and anther pores that are dorsally inclined.

Chaetolepis alpina is unlike *C. perijensis* var. *perijensis* in having ovate, 3-nerved leaf blades, crenulate leaf margins, and the elevated primary vein on the abaxial leaf surface beset with sessile glands and smooth eglandular trichomes. In addition, the cauline nodes have smooth eglandular trichomes and lack glands altogether.

Representative specimens examined: **COLOMBIA.** César: Serranía de Perijá, Municipio Manaure, Cerro del Avión, en Páramo Levantamientos, Rangel *et al.* 11181 (COL); Serranía del Perijá, Municipio Manaure, Casa de Vidrio, Rangel *et al.* 11007 (COL). Magdalena: Sierra de Perijá, E of Manaure, Sabana Rubia, páramo, 3000–3100 m, Cuatrecasas & Castaneda 25082 (COL, US); Sierra de Perijá, ENE of Manaure, páramo, 1 km from the Venezuelan border, 3000 m, Grant 10870 (US).

9. *Chaetolepis perijensis* Wurdack var. *glandulosa*, Wurdack, Phytologia 41:1. 1978. (Fig. 20 D2). TYPE: VENEZUELA. ZULIA: Distrito Perijá, 5 km N of Buena Vista, at the base of cliffs along the international boundary from Hacienda Buena Vista to the N side of Cerro Laminado to the headwaters of Río Apon; Sierra de Perijá, Serranía de Valledupar, 3300–3650 m, 9–10 Jul 1974, S.S. Tillett & K.W. Hönl 747-946 (HOLOTYPE: US!).

Erect, much branched subshrub to 30 cm tall. Distal cauline internodes quadrangular, winged, glabrous or minutely furfuraceous and sparsely covered with stalked glandular trichomes and sessile glands. Older branches woody, the bark furrowed with age. Principal leaves coriaceous and spreading; adaxial leaf surface minutely furfuraceous and with sessile glands when dry; abaxial leaf surface glandular-punctate; blades 4–7.5 × 1–1.5 mm, oblong, obtuse to rounded apically, obtuse or broadly acute basally, the single primary nerve extending the entire length of the blade; margins obscurely ciliolate-serrulate, the cilia 0.1–0.2 mm long, appressed and often caducous; petioles 0.3–0.8 × 0.4–0.5 mm, glabrous. Flowers terminal and solitary, often on lateral branches. Bracts 3–4 × 0.6–1 mm, similar to principal leaves but smaller, petioles 0.5–1 × 0.4–0.5 mm, glabrous. Floral pedicels 0.6–1.0 mm long. Hypanthia (at anthesis) 3–4 × 2.5–3 mm, urceolate to narrowly campanulate, moderately to densely covered with sessile glands, appearing somewhat minutely furfuraceous when dry and moderately covered with glandular trichomes; hypanthia (at maturity) with vascular ribs conspicuous when dry. Calyx lobes 0.8–1.2 × 0.9–1.1 mm, erect, lance-triangular to deltoid, acute apically, margins ciliate; calyx lobes glandular and appearing minutely furfuraceous when dry; intercalycine lobe sinuses with a single eglandular trichome. Petals 4–5 × 2–3 mm, yellow, entire, glabrous, apex acute to obtuse and lacking a terminal trichome. Filaments 3–4 mm long, yellow; anthers 1.5–2 × 0.25–0.5 mm, linear; pore dorsally inclined; connective prolonged 0.1–0.2 mm below the thecae. Ovary apex sparsely to moderately covered with smooth eglandular trichomes; style 9–10 mm long, yellow to magenta. Seeds 0.7–1 mm long, brown. Chromosome number: unknown.

Flowering.—July.

Habitat and Distribution (Fig. 21).—Known only from the type locality where it occurs in areas with sparse, low lying vegetation, on rocks and cliff bases at 3300–3650 m.

Discussion.—The holotype was the only collection available for study so no critical assessment of its taxonomic status is possible. This variety differs from the nominate one by its hypanthial indument (Fig. 20 D2) and geographic distribution. *Chaetolepis perijensis* var. *glandulosa* has hypanthia with sessile glands intermixed with smooth glandular trichomes while *C. perijensis* var. *perijensis* has a hypanthium with only sessile glands. Both varieties occur on the Sierra de Perijá which extends along the northeastern border of Colombia and Venezuela, but *Chaetolepis perijensis* var. *glandulosa* is found at 3300–3650 m and the nominate variety grows at 3000–3350 m. Further study of these populations is needed to determine whether the above mentioned differences are consistent and worthy of formal taxonomic recognition.

10. *Chaetolepis phelpsiae* Gleason var. *phelpsiae*, Brittonia. 7:82.1950. (Figs. 22 A–D1; E1, E2). TYPE: VENEZUELA. AMAZONAS: Cerro Yavi, elev. 1400 m, 1–3 Mar 1947, K.D. Phelps & C.B. Hitchcock 27 (HOLOTYPE: NY!).

Compactly branched subshrub 10–30 cm tall. Distal cauline internodes quadrate, somewhat winged, sparsely covered with spreading, glandular and eglandular trichomes 1–1.5 mm long. Cauline nodes similar to internodes but with a moderate to dense covering of eglandular trichomes 1–2 mm long. Older internodes terete,



FIG. 21. Distributions of *Chaetolepis perijensis* var. *perijensis*, *C. perijensis* var. *glandulosa*, *C. phelpsiae* var. *phelpsiae*, *C. phelpsiae* var. *chimantensis*, *C. santamartensis*, and *C. sessilis*.

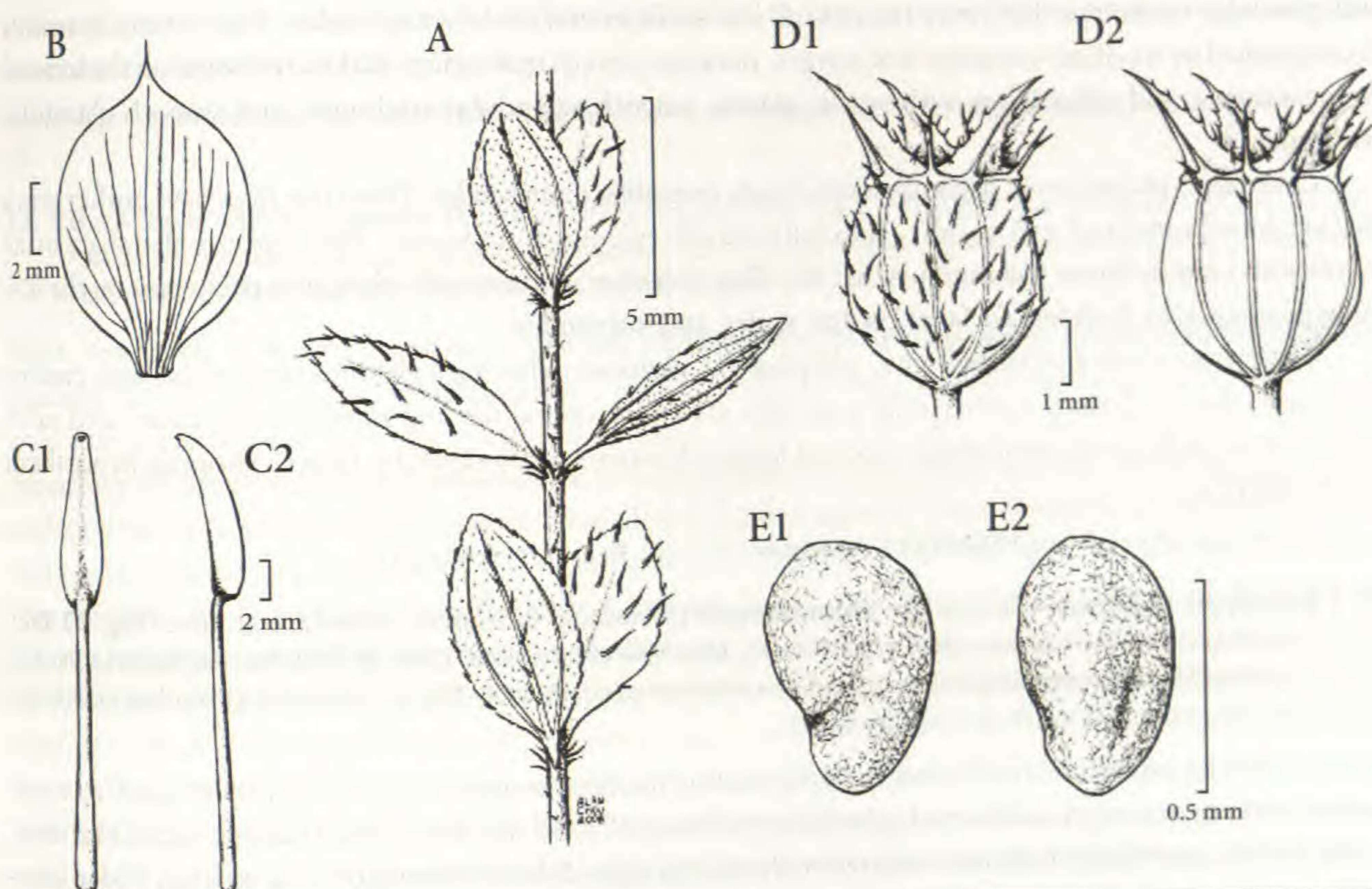


FIG. 22. *Chaetolepis phelpisiae* var. *phelpisiae*. A. Habit. B. Petal (adaxial surface). C1. Stamen (dorsal view). C2. Stamen (profile view). D1. Hypanthium. E1. Seed (profile view). E2. Seed (ventral view). *Chaetolepis phelpisiae* var. *chimantensis*. D2. Hypanthium (A, B, C1, C2, D1, E1, E2 from Phelps & Hitchcock 6, NY; D2 from Wurdack 521, F, NY, US).

woody, glabrous, exfoliating with age. Principal leaves coriaceous and spreading; adaxial surface sparsely to moderately covered with antrorsely spreading, eglandular trichomes on the upper two-thirds of the blade, sometimes glabrous; abaxial surface glandular-punctate and also sparsely covered with glandular and eglandular trichomes between the primary and secondary veins, sparsely beset with eglandular and glandular trichomes on the primaries and secondaries; blades 7–15 × 2–5.5 mm, lanceolate to ovate, acute apically, cuneate basally, 3–5-nerved with three innermost nerves extending the entire length of the blade and the outermost pair extending a third to half the length of the blade; margins ciliate-crenulate; petioles 1.5–2.5 mm long, pair extending a third to half the length of the blade; margins ciliate-crenulate; flowers terminal, solitary or in simple 3-flowered dichasia. Bracts 4.5–9 × 1.5–3.5 mm, like the principal leaves but smaller; petioles 0.5–1 × 0.3–0.4 mm. Floral dichasia. Bracts 4.5–9 × 1.5–3.5 mm, like the principal leaves but smaller; petioles 0.5–1 × 0.3–0.4 mm. Hypanthia (at anthesis) 3–4 × 2–3 mm, campanulate to suburceolate, pedicels 0.25–0.5 mm long, glabrous. Hypanthia (at maturity) with vascular ribs prominent when dry. Calyx lobes 2–2.5 × 1–1.5 mm, erect or ascending, narrowly deltoid, apically acute, ciliate, beset with sessile glands and a sparse cover of smooth eglandular trichomes and smooth glandular trichomes; intercalycine lobe sinus with a bifurcate trichome, sometimes also with one or two smooth eglandular unbranched trichomes 1–2 mm long. Petals 5–8 × 4–5 mm, yellow, margins entire, two smooth eglandular unbranched trichomes 1–2 mm long. Filaments 5–6.5 mm long, yellow; anthers 4–5 × 0.3–0.5 mm, yellow, apex cuspidate with a terminal trichome. Connective minutely prolonged below the thecae 0.2–0.3 mm, yellow, linear to arcuate; pore dorsally inclined; style 7–12 mm long, yellow. Seeds 0.4–0.6 mm long, pale brown. Chromosome number: unknown.

Flowering.—March.

Habitat and Distribution (Fig. 21).—Known only from Cerro Yavi in Amazonas state, Venezuela, on rocks and sandstone cliffs at 1400–1900 m.

Discussion.—*Chaetolepis phelpisiae* var. *phelpisiae* is a much branched subshrub with smooth eglandular

and glandular trichomes that cover the abaxial leaf surfaces and cauline internodes. This variety is readily distinguished by its ciliate-crenulate leaf margin, punctate abaxial leaf surface, forked trichome on the intercalycine sinuses, and calyx lobes with sessile glands, smooth eglandular trichomes and smooth glandular trichomes.

Chaetolepis phelpsiæ var. *phelpsiæ* most closely resembles *C. anisandra*. These two taxa have anther pores that are dorsally inclined, and an ovary apex with smooth eglandular trichomes. These species also share ovate leaves with cuneate bases; leaf margins that are ciliate-crenulate; and smooth eglandular trichomes on the distal hypanthial area, both leaf surfaces, cauline nodes, and internodes.

Chaetolepis anisandra differs from *C. phelpsiæ* var. *phelpsiæ* in having a glabrous hypanthial base; cauline internodes that are densely covered with a mixture of smooth eglandular and glandular trichomes; and calyx lobes that are glabrous. It consistently occurs at higher elevations (2100–3400 m) than *C. phelpsiæ* in northern South America.

Representative specimen examined: VENEZUELA. Amazonas: Cerro Yavi, Phelps & Hitchcock 6 (NY).

11. *Chaetolepis phelpsiæ* Gleason var. *chimantensis* (Wurdack) Grimm & Almeda, stat. nov. (Fig. 22 D2).

Chaetolepis phelpsiæ Gleason ssp. *chimantensis* Wurdack, Mem. New York Bot. Gard. 10(5):138. 1964. TYPE: VENEZUELA. BOLIVAR: Chimantá Massif, frequent along lower escarpment face of Sarven-tepui, elev. 1900–2050 m, 13 Jan 1953, J.J. Wurdack 34108 (HOLOTYPE: US!; ISOTYPES: GH, K!, NY, P!, U, internet image!).

Much-branched subshrub 10–30 cm tall. Distal cauline internodes quadrangular, slightly winged, sparsely covered with spreading glandular and eglandular trichomes 0.5–0.7 mm long. Distal cauline nodes like internodes except moderately to densely covered with smooth eglandular trichomes 0.5–1 mm long. Older internodes terete, woody, glabrous and exfoliating with age. Principal leaves coriaceous, somewhat unequal in size in each pair, spreading; adaxially sparsely covered with spreading, smooth eglandular trichomes or glabrous; abaxially punctate between the primary and secondary veins and with a sparse cover of glandular and eglandular trichomes on the actual surface; primary and secondary veins with glandular and eglandular trichomes; blades 7–16 × 4–11 mm, ovate, elliptic-ovate to orbicular-ovate, acute apically, cuneate basally, with three or five elevated veins abaxially (three that extend the entire length of the blade and two that arise at the base and extend for one third to one half the length of the blade); margins ciliate-crenulate; petioles 0.5–2.5 mm long, sparsely covered with smooth eglandular or glandular trichomes. Flowers terminal, solitary or borne in a simple 3-flowered dichasium, bracts and bracteoles 6–10 × 3–4.5 mm, like principal leaves but smaller in size. Floral pedicels 0.5–1 mm long, glabrous. Hypanthium (at anthesis) 3.5–5 × 2.5–4 mm, urceolate, upper half sparsely covered with scattered appressed or spreading, smooth eglandular (sometimes glandular) trichomes, lower half glabrous; hypanthia (at maturity) with vascular ribs prominent and conspicuous when dry. Calyx lobes 2–2.5 × 1–1.5 mm, deltoid to lance-triangular, apically acute, erect or spreading, ciliate, beset with sessile glands and a sparse cover of smooth glandular and eglandular trichomes both on and off the midrib, persistent; intercalycine lobe sinus with a forked trichome. Petals 7–10 × 4–5 mm, yellow, margins entire, glabrous, apex cuspidate with a terminal trichome. Filaments 7–9 mm long, yellow; anthers 2.5–3 × 0.4–0.5 mm, yellow, linear to arcuate; pore dorsally inclined, connective prolonged 0.2–0.3 mm below the thecae. Ovary apex sparsely to moderately covered with smooth eglandular trichomes; style yellow, 10–15 mm long. Seeds 0.5–0.6 mm long, pale brown. Chromosome number: unknown.

Flowering.—January through March.

Habitat and Distribution (Fig. 21).—*Chaetolepis phelpsiæ* var. *chimantensis* is known only from eastern Venezuela on the Chimantá Massif at the upper falls of Río Tirica and the lower escarpment and talus forest of Sarven-tepui from 1900–2050 m.

Discussion.—Few collections of *Chaetolepis phelpsiæ* var. *chimantensis* are known but it is readily distinguished from *C. phelpsiæ* var. *phelpsiæ* by several characters. A major portion of the hypanthium is glabrous while the apical region is sparsely beset with smooth eglandular trichomes (Fig. 22 D2). *Chaetolepis phelpsiæ* var. *phelpsiæ* has a hypanthium covered throughout with smooth eglandular trichomes. *Chaetolepis phelpsiæ* var. *chimantensis* has ovate, 5-nerved leaf blades whereas *C. phelpsiæ* var. *phelpsiæ* has lanceolate leaf blades

that are 3-nerved. An evaluation of the differences between these varieties will be necessary when more and better material becomes available for study.

Representative specimens examined: **VENEZUELA. Bolivar:** vicinity of upper falls of Río Tirica above summit camp, Wurdack 521 (F, NY, US).

12. *Chaetolepis santamartensis* Wurdack, *Phytologia* 8:165. 1962. (**Fig. 23**). TYPE: COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, SE slopes, Hoya del Río Donachuí, near Col, 3070–3100 m, subpáramos, 9 Oct 1959 (fl, fr), J. Cuatrecasas & R.R. Castaneda 24669 (HOLOTYPE: US!; ISOTYPE: COL, internet image!).

Erect, compactly branched shrub up to 2 m tall. Older internodes woody, terete. Distal cauline internodes quadrate and densely covered with spreading, elongate, slightly roughened trichomes 0.5–1.0 mm long. Principal leaves membranaceous and somewhat unequal in size in each pair; adaxial surface with antrorsely spreading, minutely roughened trichomes ca. 0.5 mm long evenly distributed over the entire surface; abaxial surface with erect, slightly roughened trichomes 0.4–0.8 mm long evenly distributed on and between the primary and secondary veins; blades 10–15 × 3–7 mm, ovate, elliptic to obovate, apex broadly acute to obtuse, base rounded, 5(–7)-plinerved with the three innermost nerves extending the entire length of the blade and the outermost pair extending one third to two thirds the length of the blade; margins entire to obscurely ciliate-crenulate; petioles 0.5–1.5 × 0.5 mm, densely covered with erect, slightly roughened trichomes. Flowers terminal, solitary or in simple 3-flowered dichasia. Bracts and bracteoles 4–6 × 3–4 mm, like principal leaves but smaller, petioles 0.4–0.6 × 0.2–0.3 mm. Flowers sessile or on pedicels 1–2 mm long, densely covered with spreading, slightly roughened trichomes. Hypanthia (at anthesis) 3–4 × 3.5–4 mm, campanulate, moderately covered at the base with erect slightly roughened trichomes, upper two-thirds glabrous; hypanthia (at maturity) with vascular ribs only faintly visible when dry. Calyx lobes 1.5–2.5 × 2.5–3 mm, erect to spreading varying to reflexed, broadly deltoid, rounded apically, sparsely to moderately covered with erect slightly roughened trichomes, margins ciliate. Intercalycine lobe sinus with one to three barbellate trichomes. Petals 6–9 × 3–5 mm, magenta, margins ciliate and erose, apically obtuse. Filaments 4–6 mm long, magenta; anthers 2–3 × 0.5–0.8 mm, yellow, linear-oblong; pore slightly inclined dorsally. Connective not prolonged below thecae but with a single deflexed thickening dorso-basally. Ovary apex densely covered with slightly roughened trichomes; style 7–9 mm long, magenta, erect. Seeds 1 mm long, brown. Chromosome number: unknown.

Flowering.—October.

Habitat and Distribution (Fig. 21).—This species occurs on the southeastern slopes of the Sierra Nevada de Santa Marta of Colombia in Andean forests and subpáramos at 2500–3300 m.

Discussion.—Only five collections of *Chaetolepis santamartensis* are known but it is distinctive and readily recognized. It is a sizable shrub or subshrub with prevailingly 5-plinerved leaf blades and a copious indument of spreading roughened trichomes on uppermost internodes and on both leaf surfaces (Fig. 23).

Chaetolepis santamartensis shares some similarities with *C. microphylla*. Both species have entire ciliate leaf blades, compound dichasia, and roughened trichomes covering the internodes, nodes, and leaves.

Chaetolepis microphylla differs from *C. santamartensis* by its small ovate leaves (2–6 × 2–4 mm), glabrous hypanthial base, and elongate moderately roughened to dendritic trichomes covering the internodes, nodes, and leaves. *Chaetolepis microphylla* has anthers with ventrally inclined (vs. slightly dorsally inclined) pores, and leaves that have three veins that extend from the base of the blade to its apex, and yellow (vs. magenta) eciliate petals.

Representative specimens examined: **COLOMBIA. César:** Sierra Nevada de Santa Marta, Valledupar, páramo entre Mamancana y Nabusi-make, Carbonó 3657 (UTMC). **Magdalena:** Sierra Nevada de Santa Marta, valle del Río Donachuí, van der Hammen 1156 (COL); Sierra Nevada de Santa Marta, transecto del Alto Río Buritaca, Jaramillo et al. 5434 (COL); Sierra Nevada de Santa Marta, Alto Buritaca, Rangel & Cleef 908 (COL).

13. *Chaetolepis sessilis* Pittier, *J. Wash. Acad. Sci.* 13:385. 1923. (**Fig. 24**). TYPE: VENEZUELA. MÉRIDA: Páramo de Aricagua, 3200 m, 31 Mar 1922, A. Jahn 1037 (HOLOTYPE: VEN, internet image!; ISOTYPES: G!, GH!, NY!, US).

Compactly branched subshrub 20–30 cm tall. Distal cauline internodes subquadrate, winged or carinate, sparsely to moderately covered with sessile glands. Distal cauline nodes like internodes but sparsely covered

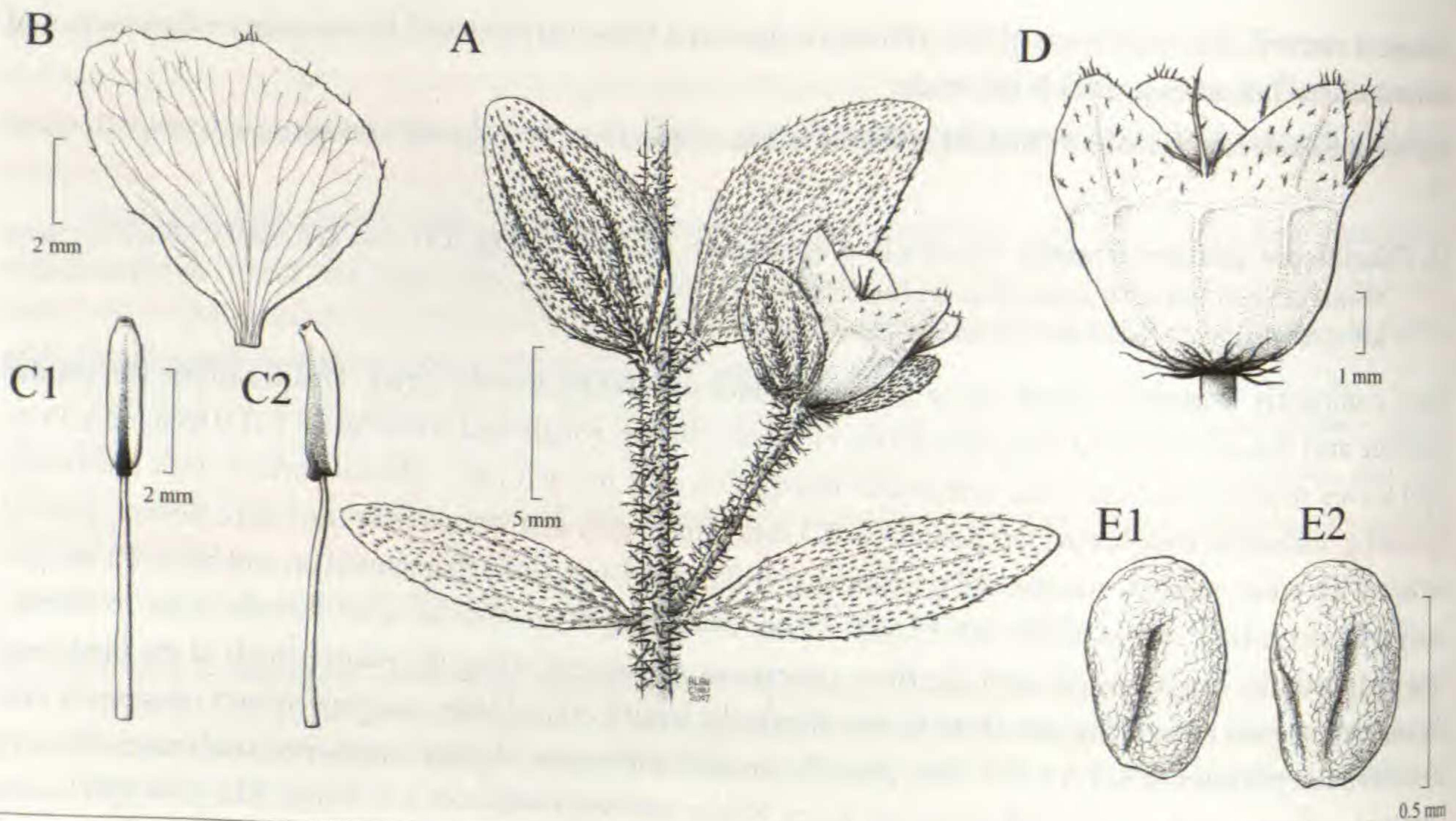


FIG. 23. *Chaetolepis santamartensis*. A. Habit. B. Petal (adaxial surface). C1. Stamen, dorsal view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from van der Hammen 1156, COL).

with smooth, eglandular, antrorsely spreading or appressed trichomes 1–1.5 mm long. Older internodes woody, terete and furrowed with age. Principal leaves coriaceous and spreading; adaxial foliar surface glabrous; abaxial foliar surface glabrous on the primary and secondary veins and punctate between them; blades 5–10 × 1.5–4.5 mm, elliptic to oblong-elliptic, acute apically and basally, 3-nerved; margins serrulate and eciliate, sessile. Inflorescence usually a terminal, simple dichasium. Bracts much like principal leaves. Bracteoles 2.5–3.5 × 1–1.5 mm, narrowly elliptic to narrowly obovate, acute apically and basally, glabrous abaxially, punctate between the primary and secondary veins and glabrous on the actual elevated veins; subsessile or with petioles 0.3–0.5 mm long. Floral pedicels 1–2 mm long, beset with sessile glands. Hypanthia (at anthesis) 4.5–8 × 2.5–3.5 mm, urceolate, moderately covered with sessile glands and sparsely to moderately covered with appressed, eglandular trichomes; hypanthia (at maturity) with conspicuously elevated vascular ribs. Calyx lobes 1.5–2.5 × 0.8–1.2 mm, lance-deltoid, apically acute, ascending, sometimes spreading or reflexed, ciliate; calyx lobes moderately covered with sessile glands both on and off the midrib; intercalycine lobe sinus with bifurcate or trifurcate trichomes. Petals 5–6 × 3.5–4.5 mm, yellow, margins entire, glabrous, apically cuspidate with a terminal trichome. Filaments 5–6 mm long, yellow; anthers 3.5–4 mm long, yellow, linear to arcuate; pore ventrally inclined; connective prolonged 0.5–0.8 mm below the thecae. Ovary sparsely covered with appressed smooth eglandular trichomes; style 5–7 mm long, yellow. Seeds 0.4–0.6 mm long, brown. Chromosome number: unknown.

Flowering.—March to June.

Habitat and Distribution (Fig. 21).—Known only from Mérida, Venezuela, in Don Pedro and Aricagua páramos at 2800–3300 m.

Discussion.—Only two collections of *Chaetolepis sessilis* were available for study. Despite limited material, this species is readily distinguished by a variety of characters. It has smooth eglandular trichomes on the abaxial leaf surface between the primary and secondary veins, cauline nodes, and hypanthia. It also has sessile glands on the cauline internodes, calyx lobes, and hypanthia, 3-nerved blades that are serrulate and eciliate, a bifurcate or trifurcate trichome at each intercalycine sinus, and a ventrally inclined anther pore (Fig. 24).

The closest relative of *Chaetolepis sessilis* appears to be *C. perijensis* var. *perijensis*. Both species have ses-

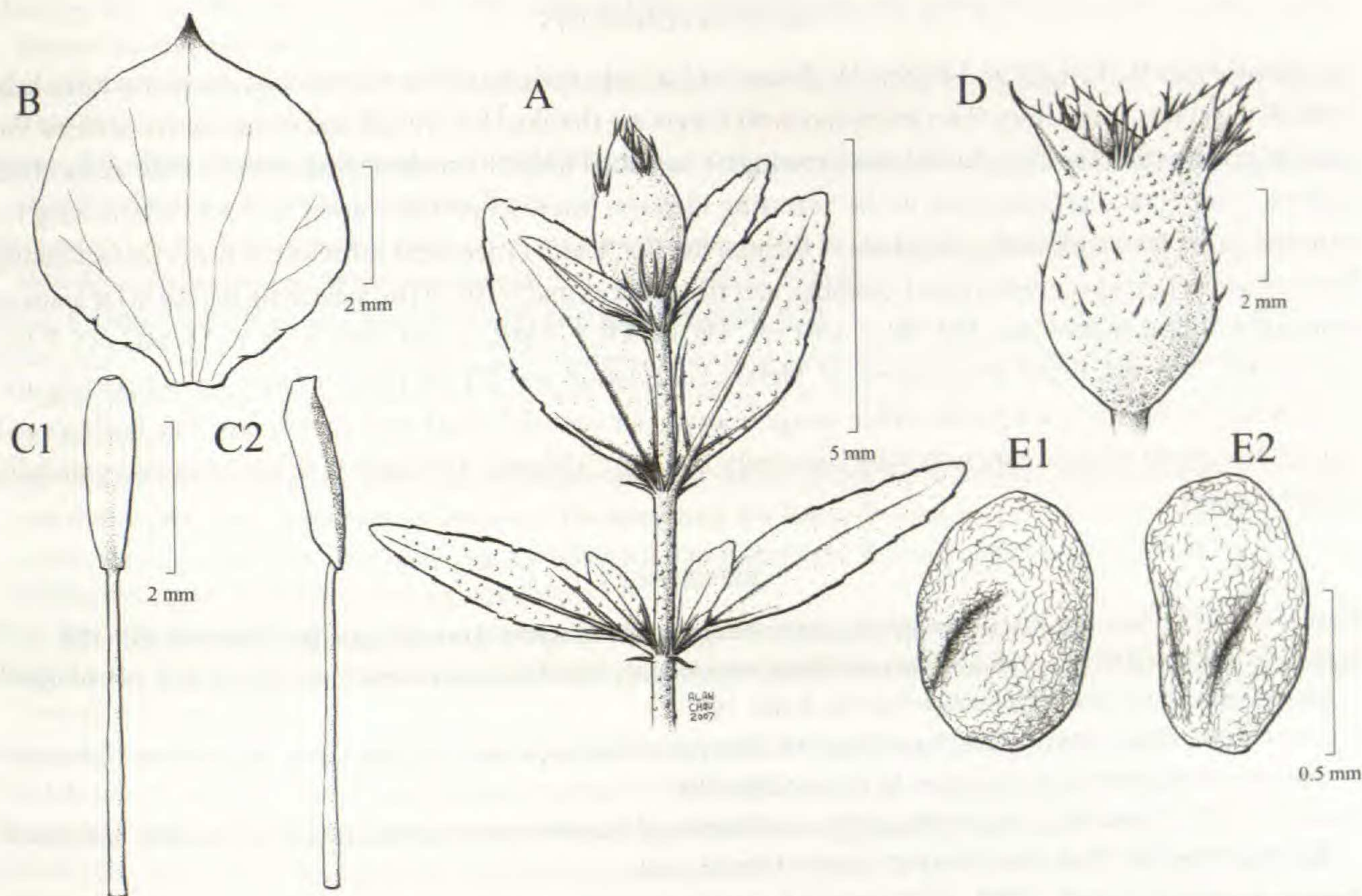


FIG. 24. *Chaetolepis sessilis*. A. Habit. B. Petal (adaxial surface). C1. Stamen, ventral view. C2. Stamen, profile view. D. Hypanthium. E1. Seed, profile view. E2. Seed, ventral view (A–E2 from Ruiz-Terán & López-Figueiras 8658a, F).

sile glands on the cauline internodes, calyx lobes, and hypanthia. They also share smooth eglandular trichomes on the abaxial leaf surface between the primary and secondary veins and on the cauline nodes.

Chaetolepis perijensis var. *perijensis* is unlike *C. sessilis* in having leaf blades with a single primary vein; its leaf margins are ciliate and entire; the adaxial leaf surfaces and cauline nodes are covered with sessile glands; the abaxial leaf surface is punctate. Furthermore, the hypanthium is glabrous, the intercalycine sinuses have smooth eglandular trichomes, and the anther pore is dorsally inclined.

Representative specimens examined: **VENEZUELA. Mérida:** Páramo de Don Pedro, unos 20–22 kms al ESE de la población de El Morro, distrito Libertador, Ruiz-Terán & López-Figueiras 8658a (F, US).

EXCLUDED SPECIES

- Chaetolepis cubensis* (A. Rich.) Triana, Trans. Linn. Soc. London 28:51. 1871. BASIONYM: *Arthrostemma cubense* A. Rich., in Sagra, Hist. Fis. Cuba, Bot. 10:550. 1845. TYPE: CUBA: de la Sagra s.n. (HOLOTYPE: P!; ISOTYPES: BR!, G!, GH, MO!). *Chaetogastra cubensis* (A. Rich.) Griseb., Cat. Pl. Cub. 103. 1866. = *Tibouchina cubense* (A. Rich.) M. Gómez, Anales Hist. Nat. 23:68. 1894.
- Chaetogastra cubensis* var. *brevistrigillosa* Griseb., Cat. Pl. Cub. 103. 1866. TYPE: CUBA: Savana del Ciego, Wright 2529 (HOLOTYPE: GOET, internet image!; ISOTYPES: BR!, G!, GH!, K, internet image!, MO!, P, internet image!). *Chaetolepis saturaeioides* var. *brevistrigillosa* (Griseb.) Triana, Trans. Linn. Soc. London 28:51. 1871. *Chaetolepis brevistrigillosa* (Griseb.) Cogn., in A.DC. & C.DC., Monogr. Phan. 7:172. 1891.
- Chaetogastra organoides* Griseb., Cat. Pl. Cub. 103. 1866. TYPE: CUBA: Wright 2530 (HOLOTYPE: GOET, internet image!; ISOTYPE: K, internet image!).
- Chaetogastra saturejoides* Griseb. Cat. Pl. Cub. 103. 1866. TYPE: CUBA: Wright 2531 (HOLOTYPE: GOET, internet image!; ISOTYPES: BR!, G!, MO!, P!). *Chaetolepis saturejoides* (Griseb.) Triana, Trans. Linn. Soc. London 28:51. 1871.
- Pleroma squamatum* C. Wright, Anal. Acad. Ci. Habana 6:73. 1869. *Tibouchina squamata* (C. Wright) M. Gómez, Anales Hist. Nat. 23:68. 1894. TYPE: CUBA: Wright 3559 (HOLOTYPE: GH).
- Chaetolepis grisebachii* Cogn., in A.DC. & C.DC., Monogr. Phan. 7:172. 1891. TYPE: CUBA: Wright 2528 (HOLOTYPE: GOET; ISOTYPES: MO, internet image!, S, internet image!).

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REFERENCES

- ALMEDA, F. 1997a. Chromosomal observations on the Alzateaceae (Myrtales). *Ann. Missouri Bot. Gard.* 84:305–308.
- ALMEDA, F. 1997b. Chromosome numbers and their evolutionary significance in some neotropical and paleotropical Melastomataceae. *BioLlania Edición Esp. No.* 6:167–190.
- ALMEDA, F. 2001. *Chaetolepis*. In: J.A. Steyermark, P.E. Berry, K. Yatskievych, and B.K. Holst, eds. *Flora of the Venezuelan Guayana*. Missouri Botanical Garden, St. Louis. 6:294–295.
- ALMEDA, F. 2013. Systematic and phylogenetic significance of chromosome number diversity in some neotropical Melastomataceae. *Mem. New York Bot. Garden* 108:155–177.
- ALMEDA, F. AND T.I. CHUANG. 1992. Chromosome numbers and their systematic significance in some Mexican Melastomataceae. *Syst. Bot.* 17:583–593.
- ALMEDA, F. AND O.R. ROBINSON. 2011. Systematics and phylogeny of *Siphanthera* (Melastomataceae). *Syst. Bot. Monogr.* 93:1–101.
- BERRY, P.E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). *Ann. Missouri Bot. Gard.* 69:1–198.
- BOLKHOVSKIKH, Z., V. GRIF, T. MATEJEVA, AND O. ZAKHARYEVA. 1969. Melastomataceae. In: A.A. Federov, ed. *Chromosome numbers of flowering plants*. V.L. Komarov Botanical Inst., Academy of Sciences of the U.S.S.R., St. Petersburg. P. 430.
- BRADLEY, M.V. 1948. An aceto-carminic squash technic for mature embryo sacs. *Stain Technol.* 23:29–40.
- COGNIAUX, A. 1891. Mélastomacées. In: A. and C. de Candolle, eds. *Monographiae phanerogamarum*. G. Masson, Paris. 7:1–1256.
- FAVARGER, C. 1962. Nouvelles recherches cytologiques sur les Mélastomatacées. *Ber. Schweiz. Bot. Ges.* 72:290–305.
- FREIRE-FIERRO, A. 2002. Monograph of *Aciotis* (Melastomataceae). *Syst. Bot. Monogr.* 62:1–99.
- GANSSE, A. 1955. Ein Beitrag zur Geologie und Petrographie der Sierra Nevada de Santa Marta (Kolumbien, Südamerika). *Schweiz. Min. Pet. Mitt.* 35:209–279.
- GIVNISH, T.J., K.C. MILLAM, T.M. EVANS, J.C. HALL, J.C. PIRES, P.E. BERRY, AND K.J. SYTSMA. 2004. Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and South American-African disjunctions in Rapateaceae and Bromeliaceae based on *ndhf* sequence data. *Int. J. Pl. Sci.* 165:35–54.
- GRAHAM, S.A., K. OGINUMA, P.H. RAVEN, AND H. TOBE. 1993. Chromosome numbers in *Sonneratia* and *Duabanga* (Lythraceae s.l.) and their systematic significance. *Taxon* 42:35–41.
- HAMMEN, T. VAN DER. 1961. Late Cretaceous and Tertiary stratigraphy and tectogenesis of the Colombian Andes. *Geol. Mijnbouwkd.* 40:181–188.
- IRVING, E. 1975. Structural evolution of the northernmost Andes, Colombia. *Geol. Survey Professional Paper* 846:1–47. United States Government Printing Office, Washington, D.C.
- JACQUES-FÉLIX, H. 1994 [1995]. Histoire des Melastomataceae d'Afrique. *Bull. Mus. Hist. Nat., ser. 4, sect. B, Adansonia* 16(2–4):235–311.
- JOHNSON, L.A.S. AND B.G. BRIGGS. 1984. Myrtales and Myrtaceae – a phylogenetic analysis. *Ann. Missouri Bot. Gard.* 71:700–756.
- LEÓN, H. AND H. ALAIN. 1974. *Chaetolepis*. In: *Flora de Cuba*. Otto Koeltz Science Publishers, Koenigstein. 2:12–13.
- LINCOLN, F.C., S.R. PETERSON, AND L. ZIMMERMAN. 1998. The migration of birds. *United States Fish and Wildlife Service Cir.* 16:1–113.

- MADDISON, D.R. AND W.P. MADDISON. 2000. MacClade: analysis of phylogeny and character evolution, version 4.0PPC. Sinauer, Sunderland, MA.
- MARTIN, C.V. AND G. CREMERS. 2007. Les Melastomataceae américaines décrites par C. Naudin. *J. Bot. Soc. Bot. France* 37:3–111.
- MARTINS, A.B. 1989. Revisão taxonômica do gênero *Marcetia* (Melastomataceae). Dissertação de Doutorado, Universidade Estadual de Campinas, Campinas, Brazil.
- MICHELANGELI, F.A., P.J. GUIMARÃES, D.S. PENNEYS, F. ALMEDA, AND R. KRIEBEL. 2013. Phylogenetic relationships and distribution of New World Melastomeae (Melastomataceae). *Bot. J. Linn. Soc.* 171:38–60.
- MIQUEL, F. 1840. *Chaetolepis*. In: *Commentarii Phytographici*. Leyden. P. 72.
- PENNEYS, D.S., F. ALMEDA, AND F.A. MICHELANGELI. 2010. Progress towards a comprehensive phylogenetic analysis and revised classification of the Melastomataceae. Scientific Abstracts no. 509. Botany 2010, July 31–August 4, Providence, Rhode Island.
- RANGEL-CH., J.O. AND A. GARZÓN-C. 1997. Sierra Nevada de Santa Marta, Colombia. In: *Centres of plant diversity: A guide and strategy for their conservation (Volume 3, The Americas)*, S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villalobos, and A.C. Hamilton, eds. WWF-World Wildlife Fund for Nature and IUCN-The World Conservation Union. IUCN Publications Unit, Cambridge, U.K. Pp. 426–430.
- RAVEN, P.H. 1975. The bases of angiosperm phylogeny: Cytology. *Ann. Missouri Bot. Gard.* 62:724–764.
- RENNER, S.S. AND K. MEYER. 2001. Melastomeae come full circle: Biogeographic reconstruction and molecular clock dating. *Evolution* 55:1315–1324.
- SIMPSON, B.B. 1975. Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* 1:273–294.
- SOLT, M.L. AND J.J. WURDACK. 1980. Chromosome numbers in the Melastomataceae. *Phytologia* 47:199–220.
- STANDLEY, P.C. 1938. Melastomataceae. In: *Flora of Costa Rica*. Field Mus. Nat. Hist., Bot. Ser. 18:783–845.
- SWOFFORD, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (and other Methods). Ver. 4.0b10. Sinauer Associates, Sunderland, MA.
- THIERS, B.M. 2012. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- THORNE, R.F. 1973. Floristic relationships between tropical Africa and tropical America. In: B.J. Meggers, E.S. Ayensu, and W.D. Duckworth, eds. *Tropical forest ecosystems in Africa and South America: A comparative review*. Smithsonian Institution Press. Washington, DC. Pp. 27–47.
- THORNE, R.F. 1992. Classification and geography of the flowering plants. *Bot. Rev.* 58:225–348.
- TODD, W.E.C., AND M.A. CARRIKER, JR. 1922. The birds of the Santa Marta Region of Colombia: A study in altitudinal distribution. *Ann. Carnegie Mus.* 14:3–576.
- TODZIA, C. A. AND F. ALMEDA. 1991. A revision of *Tibouchina* section *Lepidotae* (Melastomataceae: Tibouchineae). *Proc. Calif. Acad. Sci.* 47(6):175–206.
- TRIANA, J. 1871. Les Mélastomacées. *Trans. Linn. Soc. London* 28:1–188.
- URIBE-U., L. 1972. Catálogo ilustrado de las plantas de Cundinamarca. Vol. 5. Passifloraceae, Begoniaceae, Melastomataceae. Publ. Inst. Ciencias Naturales, Bogotá, Colombia.
- WURDACK, J.J. 1973. Melastomataceae. In: T. Lasser, ed. *Flora de Venezuela*, Instituto Botánico, Caracas, Venezuela. 8:1–819.
- WURDACK, J.J. 1986. Atlas of hairs for neotropical Melastomataceae. *Smithsonian Contr. Bot.* 63:1–80.
- WURDACK, J.J., S.S. RENNER, AND T. MORLEY. 1993. Melastomataceae. In: A.R.A. Görts-van Rijn. *Flora of the Guianas*. 99:1–425. Koeltz Scientific Books, Koenigstein, Germany.